Redescription of a North Pacific Prickleback, *Alectridium auranticum*[1]

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ABSTRACT

Alectridium auranticum Gilbert and Burke, which was previously known from a single specimen and synonymized with *Alectrias alectrolophus* (Pallas), is redescribed. Many new specimens indicate that the species is readily distinguishable from the other members of the stichaeid subfamily Alectriinae by a single median interorbital head pore and the scales on the body not extending in front of the 13th anal fin ray. It is found in the lower intertidal and subtidal waters between the Commander Islands, USSR, and Kodiak, Alaska.

INTRODUCTION

Previously, *Alectridium auranticum* was known from the single specimen described by Gilbert and Burke (1912). In 1958, Makushok synonymized this representative of the stichaeid subfamily Alectriinae with *Alectrias alectrolophus* (Pallas). As part of a study of the fish fauna of the Aleutian Islands in Alaska, the Institute of Fisheries collected many specimens of *A. auranticum*. This material as well as additional collections in the United States National Museum has permitted a more detailed evaluation of this species. Although no specimens of *Alectrias gallinum* (Lindberg), *Alectrias cirratum* (Lindberg), or *Pseudoalectrias tarasovi* Lindberg were available for study, characters reported by Makushok (i.e., either absence of a median head pore or absence of scales) exclude the identity of these forms with *Alectridium*. This paper is mainly concerned with distinguishing *Alectridium* from the closely related *A. alectrolophus*, *Anoplarchus insignis* Gilbert and Burke, and *Anoplarchus purpurescens* Gill. These latter species are found in collections containing *Alectridium* and have been frequently confused with this rarer form. *Alectridium auranticum* is the only known member of its genus.

MATERIALS AND METHODS

All counts and measurements follow those of Peden (1966). Collections from the United States National Museum are indicated by USNM and collections from the Institute of Fisheries by BC. Because of great geographic variation in meristics of some of the Alectriinae, a large number of collections of each species were examined. These include the following (numbers of specimens are indicated

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within the brackets; approximate latitude and longitude are indicated after certain localities).

Alectridium auranticum. Commander Islands, USSR (Komandorski Ostrov, SSSR), 55°N and 167°E: USNM 74393 (holotype), USNM 7412 (8), BC 63-1044 (16); Attu Island, Alaska, 53°N and 173°E: BC 63-1004 (1), BC 63-1006 (5), BC 63-1011 (1); Semisopochnoi Island, 52°N and 179°45′W: USNM 70858 (1), USNM 70989 (1); Adak Island, 51°45′N and 176°30′W: BC 63-1429 (1), BC 65-30 (6); Umnak Island, 53°30′N and 168°W: BC 63-1070 (2); Unalaska Island, 54°N and 167°W: USNM 70960 (6); Egg Island, 53°53′N and 166°W: USNM 117493 (2); Kodiak, 57°45′N and 152°30′W: BC 63-1033 (1); "Coal Harbour": USNM 23955 (3). The locality label for this last collection is questionable, especially as to whether it refers to Alaska or British Columbia.

Alectrias benjamini. Japan: BC 63-1087 (2), BC 63-1088 (1), USNM 71278 (11), USNM 71415 (20), USNM 71523 (18).

Alectrias alectrolophus. Petropavlovsk, Kamchatka, USSR: USNM 38960 (4); Commander Islands: USNM 38962 (15), USNM 70967 (4), USNM 74712 (23), BC 63-1041 (14); St. Michael, Alaska 63°30′N and 162°W: USNM 22018 (6), USNM 23979 (5), USNM 32973 (6).

Anoplarchus insignis. Attu Island area: BC 65-21 (13), BC 65-8 (9), BC 65-9 (3), BC 65-29 (3); Kodiak Island: BC 65-44 (9); British Columbia: BC 62-902 (22), BC 63-736 (12), BC 63-934 (22).

Anoplarchus purpurescens. Attu Island area: BC 65-3 (28), BC 65-9 (15); Kodiak Island: BC 65-44 (8), BC 65-48 (13); British Columbia: BC 55-113 (10), BC 5-119 (13); California: BC 53-294 (20).

DIFFERENCES BETWEEN *ALECTRIDIUM* AND ITS ALLIED GENERA

Alectridium can be distinguished from other forms of the Alectriinae by the presence of a median interorbital head pore (Fig. 1) and the distribution of scales on the body (Table I). In *Alectrias* and *Anoplarchus* the interorbital pores are always paired and never occur in the midline of the head. *Alectridium* has scales extending posteriorly on the body from a point between the 13th and 25th rays of the anal fin. *Alectrias* and *Anoplarchus* usually have scales extending much more anteriorly. Counts of anal fin rays may also be used to separate *Alectridium* from some specimens of *Alectrias* and *Anoplarchus* (Table II). As indicated in Fig. 1, *Alectrias* and *Anoplarchus* often have a larger fleshy ridge or crest on the midline of the snout and interorbit.

Gilbert and Burke (1912) originally distinguished *Alectridium* by the supposed absence of the lateral lines. Makushok (1958) notes the difficulty of observing the lateral lines of the Alectriinae and found lateral line pits on all specimens labelled *Alectridium* in Soviet museums. Since no other distinguishing characters were known, he considered *A. auranticum* to be synonymous with *A. alectrolophus*. Examination of the holotype of *A. auranticum* (USNM 74393)

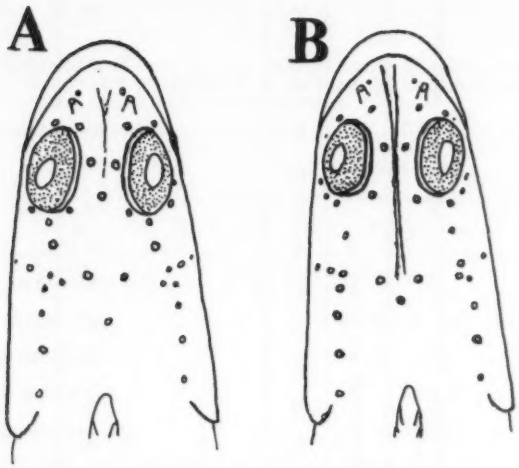

FIG. 1. Head pore pattern in: A, *Alectridium*; B, *Alectrias* and *Anoplarchus*

by the author did not reveal the presence of lateral line pits. However, if specimens are poorly preserved or have wrinkled or dried skin, these pits are difficult to see (Fig. 2). Since the lateral lines of the Alectriinae are so rudimentary they are a poor character to use for the identification of these forms.

As suggested by Table III, *Alectridium* might have some geographic variation in anal fin ray counts. Recognition of other forms of *Alectridium* is unwarranted until more extensive collections are obtained.

KEY TO THE GENERA OF THE ALECTRIINAE

A. Scales absent; palatine teeth absent.....*Pseudoalectrias* Lindberg
AA. Embedded scales present on posterior portion of body; palatine teeth present:
  B. Interorbital head pores paired, none being median; scales extending anteriorly past the 15th anal fin ray:
    C. Gill membranes fused to isthmus and usually not producing a free fold posteriorly: Attu and Pribilof Islands, Alaska to California .....*Anoplarchus* Gill
    CC. Gill membranes fused to isthmus, producing a free fold posteriorly: Northern Japan to Kamchatka and Commander Islands, USSR; also St. Michael, Alaska .....*Alectrias* Jordan and Evermann
  BB. A single median interorbital head pore present, other interorbital pores paired; scales not extending anteriorly past the 13th anal fin ray: Commander Islands, USSR to Kodiak, Alaska.....*Alectridium* Gilbert and Burke

REDESCRIPTION OF *ALECTRIDIUM AURANTICUM*

Counts and measurements are presented in Table IV.

Head slightly compressed. Snout steep, round in profile. Small narrow fleshy crest in midline between snout and occiput of largest specimens; when

TABLE I. Frequencies of the anterior limit of scales in *Anoplarchus*, *Alectrias*, and *Alectridium*. The numbers of specimens of each species examined are indicated within the parentheses.

	Anal ray in front of which scales do not extend																									
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Anoplarchus purpurescens (77)	6	5	5	6	3	7	9	11	7	7	4	5	2													
Anoplarchus insignis (42)								6	5	4	11	6	3	2	2	3										
Alectrias benjamini (45)	1		1	2	13	13	10	5																		
Alectrias alectrolophus (45)					2	4	10	12	10	3	2	1	1													
Alectridium auranticum (33)														1	1	3		4	9	3	6	3	2			1

TABLE II. Frequencies of anal fin ray numbers in *Anoplarchus*, *Alectrias*, and *Alectridium*. The numbers of specimens of each species examined are indicated within the parentheses.

	Number of rays										
	36	37	38	39	40	41	42	43	44	45	46
Anoplarchus purpurescens (84)	1	6	24	25	22	6					
Anoplarchus insignis (90)					4	16	30	18	18	3	1
Alectrias benjamini (49)			1	4	15	21	8				
Alectrias alectrolophus (32)							4	14	10	4	
Alectridium auranticum (50)						4	18	20	8		

FIG. 2. *Alectridium auranticum* (BC 65-30). Specimen is 66 mm in standard length. During preservation the skin of the specimen has become unnaturally wrinkled and the anal fin is not fully expanded.

TABLE III. Geographic variation of anal fin ray number in *Alectridium*.

	Number of rays				Number of specimens examined	Mean
	41	42	43	44		
Commander Islands	1	4	12	7	24	43.04
Attu Island		3	4		7	42.57
Adak Island	2	4	3		9	42.11
Umnak to Kodiak	1	7	1	1	10	42.20

TABLE IV. Counts and measurements of *Alectridium auranticum*. Measurements are taken from left side of specimens and expressed as thousandths of the standard length. Specimens under 40 mm in standard length were not used for measurements.

		Other specimens		
	Holotype	Number of specimens examined	Mean	Range
Anal rays	43	50	42.7	41–44
Dorsal rays	62	31	61.3	59–63
Pectoral rays	11	21	11.0	11
Precaudal vertebrae	–	26	19.7	19–21
Caudal vertebrae	–	24	46.8	46–48
Total vertebrae	–	24	66.5	65–68
Anal ray in front of which scales do not extend	17	32	18.4	13–25
Standard length in mm	75.0	31	–	41.7–89.4
Head length	152	30	150	142–158
Eye diameter	33	30	32	28–43
Fleshy interorbital width	17	31	19	13–23
Preanal distance	402	33	419	391–447
Predorsal distance	158	30	150	138–167
Caudal length	85	31	97	85–106
Pectoral length	52	31	64	52–83
Body depth above anal fin	112	31	106	94–114
Body width	74	31	76	54–101
Snout	33	31	29	24–35
Longest anal ray	52	30	46	39–56
Longest dorsal ray	41	29	45	39–53

crest present, median interorbital pore on ridge of this crest. Gill membranes connected with each other and fused to isthmus so as to produce a narrow free fold. Teeth on jaws, vomer, and palatines. Nasal tube long, constricted distally; between anterior edge of orbit and snout. Head pores: usually 6 in suborbital series on each side of head, 1 anterior to each nasal tube, 3 in interorbital series on each side of head plus a single median interorbital pore, usually 7 in each postorbital series, usually 1 in occipital series on each side of head plus a single

median occipital pore on nape, usually 6 in each preopercular series, and 4 in each mandibular series. Mouth large; maxilla reaching to point below posterior half of eye.

Body elongate, slender, slightly compressed anteriorly, greatly compressed posteriorly; depth greatest near abdomen or anterior portion of anal fin. Dorsal and anal fins: moderately high, a little higher posteriorly; base long. Dorsal fin: origin over or slightly before pectoral base; posterior membrane confluent with caudal but well notched at basal portion of caudal. Anal fin: margin incised between rays, rounded posteriorly and barely joined to base of caudal fin; origin nearer snout than caudal base. Caudal fin short, rounded. Pectoral fins rounded. Pelvic fins absent. Two rudimentary lateral lines usually present anteriorly. Scales: small, cycloid, embedded; on posterior part of body and extending anteriorly to a point between the 12th and 26th anal fin rays.

Colour: usually very dark brown; often with lighter coloured fins, light colour of dorsal fin frequently extending as a serial pattern of 16 to 18 rounded notches onto back; sometimes irregular light and dark vertical streaks or blotches on side of belly; small dark marking accentuated with light colouration on anterior portion of dorsal fin (this light colour straw yellow in the Adak Island specimens, BC 65-30); posterior margin of gill cover etched in black; sometimes dark bars across lower jaw; usually a broad light bar passing posteroventrally across cheek from eye, this bar accentuated on each side by a fine line of dark pigment.

The holotype was reported by Gilbert and Burke (1912) to be "orange chrome above and saturn red below" in life, but "ochraceous, finely speckled with dark brown" when preserved in alcohol. This bright colour might have caused the original collectors to select this specimen as a new form even though dark specimens are abundant near the type locality. Rare, brightly coloured specimens of *Anoplarchus* are similarly known (Peden, 1966). Collection BC 63-1044, from Copper Island (Medney Ostrov), USSR, has one light-coloured specimen of *Alectridium* amongst 15 dark-coloured individuals. In life, this specimen might have been coloured similar to the holotype.

RELATIONSHIPS

Within the Alectriinae, *Alectridium* is intermediate between *Pseudoalectrias* and both *Alectrias* and *Anoplarchus*. The presence of palatine teeth demonstrates its affinity with the latter two genera whereas the median interorbital pore is shared only by *Alectridium* and *Pseudoalectrias*. On the other hand, the reduced area covered by scales in *Alectridium* can be considered an intermediate condition between the scaleless *Pseudoalectrias* and the relatively highly scaled *Anoplarchus* and *Alectrias*. As suggested by the key to the Alectriinae, the single generic character (absence of gill membrane fold) which separates *Anoplarchus* from *Alectrias* occasionally breaks down (Peden, 1966). This might persuade some workers to include *Alectrias* within the genus *Anoplarchus*. However, *Alectridium* is much more strongly differentiated and should be

considered more distantly related to the preceding two genera than these are with each other.

DISTRIBUTION AND HABITAT

Alectridium auranticum occurs together with *A. alectrolophus* in the Commander Islands, USSR, and with *A. insignis* and *A. purpurescens* from Attu Island to Kodiak, Alaska. Most collections of *Alectridium* are known from the shallow subtidal or the lower intertidal region. The collections from Attu Island were taken during lower low tides at locations characterized by rocks, sea urchins, and the marine algae *Alaria*. The Adak Island specimens were taken with skin-diving gear in 0 to 20 ft of water but during half tide. In Alaska, *A. auranticum* probably lives in close proximity to the habitat described for *A. insignis* (Peden, 1966); however, the collections known from Alaska are too few to determine the ecological differences between these species.

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Preservation of Fresh Whitefish with Gamma Radiation[1,2]

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ABSTRACT

This paper is an outline of a recent study which shows that the storage life of fresh whitefish (*Coregonus clupeaformis*) is extended considerably by the low levels of gamma radiation. On the basis of bacteriological and sensory evaluations, a dose of 150,000 rads proved to be the most effective treatment; the samples exposed to this level of radiation were judged acceptable up to 29 days of storage in ice. Fish treated with 75,000 rads were acceptable up to 22 days whereas those treated with 300,000 rads, though bacteriologically acceptable, received lower sensory scores throughout the experiment.

Bacteriological studies showed that unirradiated fresh samples were dominated by Gram-negative microorganisms belonging to the genera *Pseudomonas*, *Achromobacter*, and *Flavobacterium*. Samples treated with 150,000 rads showed survival of Gram-positive microorganisms belonging to the genera *Corynebacterium* and *Micrococcus* which were replaced by Gram-negative microorganisms after 29 days of storage.

INTRODUCTION

Under commercial practice, fresh whitefish stored in ice normally become unacceptable in about 2 weeks, deterioration being caused by action of psychrophilic microorganisms on the flesh and chemical breakdown of the tissue components.

Other investigators have shown that the use of gamma radiation can extend the shelf life of several fish products. For example, the storage life of haddock fillets and scallop meat can be increased up to approximately 2½ weeks at 0 C by a dose of 75,000 rads (Power et al., 1964; Power et al., 1964). In addition, the shelf life of soft-shell clam meat can be increased up to 25 days at 1 C by a dose of 350,000–550,000 rads (Connors and Steinberg, 1964).

Ronsivalli and Slavin (1965) reported a reduction of approximately 99% of microorganisms on haddock fillets after exposure to 250,000 rads. At the

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same time, higher doses of gamma radiation (300,000–500,000 rads) have caused noticeable changes in odour, texture, and appearance of other fish products such as sole, cod, plaice, herring, and crab (Ingram and Rhodes, 1962; Anon., 1962).

The present study was designed after those of Power et al. (1964; 1964) to evaluate the effects of gamma radiation on preservation of fresh whitefish stored at 0 C, and to identify the relative numbers of microorganisms surviving the radiation treatment.

MATERIALS AND METHODS

A total of 200 male whitefish (*Coregonus clupeaformis*) were employed in this study. They were selected over a period of a few days and, after being held alive in special retainers located at Clearwater Lake, Manitoba (54°05′N and 101°00′W), were caught in pound nets on the afternoon of October 26, 1965, after which all fish were packed alive in ice and shipped to Winnipeg from The Pas at 7:30 PM. The fish arrived at Winnipeg on the morning of October 27, 1965, where they were examined, dressed, washed, and placed individually in oxygen-impermeable Cryovac bags and packed in wooden boxes containing flake ice.

The equipment used for the irradiation of samples was the mobile Cobalt-60 gamma irradiation unit designed and constructed by Atomic Energy of Canada Limited (Fig. 1).

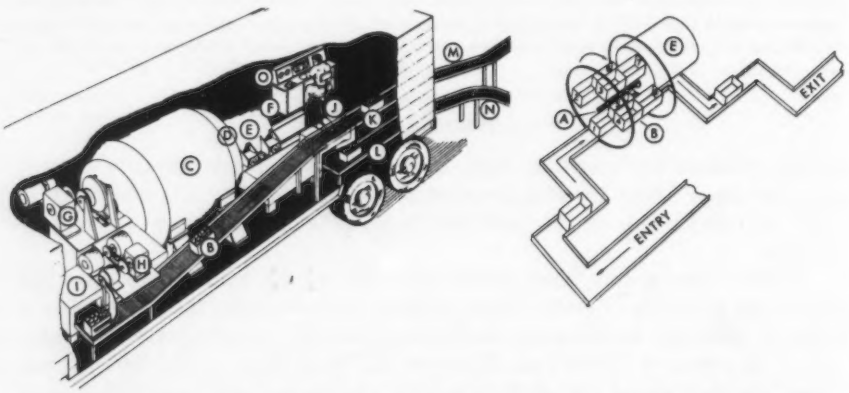

FIG. 1. Atomic Energy of Canada Ltd. mobile irradiation unit used for this study. LEGEND: A, source—cobalt 60; B, bucket; C, main shield; D, removable end; E, source mechanism and storage container; F, source positioning handle; G, drive for irradiation chamber assembly; H, drive for loading produce into entrance maze; I, entrance maze; J, drive for discharging produce onto exit conveyor; K, powered entrance conveyor; L, powered exit conveyor; M, portable powered loading conveyor; N, portable powered discharge conveyor; O, control console.

The schematic diagram on the right shows the progress of buckets inside the main shield. The assembly inside the main shield rotates in a "ferris wheel" fashion carrying four sets of two buckets around the cobalt 60. Each bucket completes two full circles around the source. The wheel stops after each quarter turn to permit a new bucket to enter and thereby push the bucket in position 5 onto the exit conveyor.

The fish were divided into five different lots as follows: (a) unirradiated control sample retained at 0 C; (b) unirradiated control sample frozen and stored at −30 C; (c) irradiated at 75,000 rads and stored in ice; (d) irradiated at 150,000 rads and stored in ice; (e) irradiated at 300,000 rads and stored in ice.

A total of four fish were placed in special aluminum boxes 20 × 20 × 37.5 cm, surrounded with flake ice, and put through the irradiation unit (10 boxes/lot). After completion of treatment, each lot of fish was packed in ice in wooden fish boxes and transferred to a storage room kept at 0 C. Samples were removed from storage for bacteriological and organoleptic analyses twice per week during the first 2 weeks, and once per week thereafter up to 5 weeks.

The bacteriological examination of samples was carried out at the Winnipeg Fish Inspection Laboratory, Department of Fisheries of Canada. Total plate counts for each lot were determined on 50-g samples. These were individually and aseptically homogenized for 2 min in sterile stainless steel Waring Blendor jars with 450 ml of sterile 0.2% peptone water. Dilutions were prepared in blanks (90 ml) of 0.2% peptone water, plated on T.G.E. (Tryptone Glucose Extract) agar medium, using duplicate plates. Subsequently, all plates were incubated at 28 C for 72 hr. Colonies were counted using a Quebec Colony Counter. Isolation of colonies was effected on the basis of their morphology and frequency after the first day, and in addition on the 16th and 29th day after irradiation. Pure culture studies were completed according to Bergey's Manual (1957), Skerman's Guide to the Identification of the Genera of Bacteria (1959), and Manual of Microbiological Methods (1957). Microscopical and biochemical studies of each isolate were undertaken for identification of various genera. For detection of possible enteric and food poisoning microorganisms, several differential media such as McGonkey's agar, E.M.B. (Eosin Methylene Blue), Staph 110, Difco Coagulase Plasma, and Tellurite Glycine Egg Yolk agar were used.

At the intervals previously stated, samples from the various lots were removed for sensory panel evaluation. The samples were examined in both the raw and cooked state. Fishery officers, experienced in the grading of fresh whitefish, examined the raw fish for odour, colour, texture, and appearance. For evaluating the cooked fish, sensory panel judges were selected from members of the Faculty of Agriculture and Home Economics at the University of Manitoba after three preliminary training sessions on judging whitefish. Two of these meetings were directed to detection of difference between fresh, frozen, and 4-day-old iced whitefish whereas the third served to acquaint the judges with the terms of the quality rating scales. A quality rating scale was employed to score each sample for odour, appearance, texture, flavour, and composite grade (Table 1). All panels were conducted with judges using individual booths in a foods laboratory at the Department of Home Economics, University of Manitoba.

Whole whitefish were baked simultaneously in five household ovens at 232 C, with each fish being placed on narrow rimmed 21.5 × 27.5 cm aluminum pans, covered with aluminum foil, and greased lightly with salad oil. These

TABLE I. Rating chart used in sensory panel evaluation.[a]

Sample Number_____

Factor						Comments
Odour	Faint	Slightly Noticeable	Noticeable	Fairly Pronounced	Pronounced	
Appearance	Desirable	Moderately Desirable	Slightly Desirable	Slightly Undesirable	Undesirable	
Texture	Desirable	Moderately Desirable	Slightly Desirable	Slightly Undesirable	Undesirable	
Flavour	Delicate	Slightly Noticeable	Noticeable	Fairly Strong	Strong	
Composite Grade	Excellent	Good	Medium	Fair	Poor	

Signature of Judge

[a]For analysis of data, numerical values were assigned to descriptive terms: e.g. 100, 80, 60, 40, 20, where 100 was most desirable and 20 the least desirable.

were baked for 10 min per inch of thickness with the exception of the frozen control, which was baked for 20 min per inch of thickness without prior thawing.

Immediately after baking, samples were taken from one side of the dorsal part of the fish and were then served in coded dishes to a panel of 7–8 judges. A set of five samples representing the five lots was presented simultaneously in a randomized order.

When testing of these sets was completed, each judge was presented with a second set of samples taken from the alternate side of the dorsal part. Thus, on each test day there were 14–16 judgments for each whitefish.

Analysis of variance following the technique outlined by Snedecor (1946) for split plot designs, was applied to each parameter measured by the sensory panel.

RESULTS AND DISCUSSION

Bacteriological Examination

The results in Table II show that the number of bacteria per gram of the irradiated fish was reduced by 89% when exposed to 75,000 rads, by 99.3% when exposed to 150,000 rads, and by almost 100% when treated with 300,000 rads. In other words, the higher the dosage the lower the bacterial count which resulted. Based on total plate counts, the fresh control unirradiated samples were unacceptable after 16 days. However, irradiated samples treated with 75,000 rads remained acceptable up to 22 days, and those treated with 150,000 rads up to 29 days whereas those samples exposed to 300,000 rads were acceptable up to 36 days of storage at 0 C. The unirradiated frozen samples were acceptable throughout the 36-day storage period and it was significant that the bacterial count was reduced by almost 100%.

Table II. Bacterial count per gram of control and irradiated whitefish stored at 0 C.

Days of storage	Control unirradiated	Control frozen	75,000 rads	150,000 rads	300,000 rads
1	100,000	47,000	11,000	716	133
5	280,000	25,000	12,000	1,600	225
8	400,000	7,000	88,000	12,000	580
12	950,000	7,000	190,000	44,000	700
16	6,800,000	4,000	400,000	58,000	1,300
22	80,000,000	4,000	1,500,000	200,000	11,000
29	–	550	5,700,000	500,000	42,000
36	–	500	–	2,300,000	1,600,000

Pure culture studies of unirradiated control samples showed that 57% of microcolonies were Gram-negative belonging to the genera *Pseudomonas*, *Achromobacter*, and *Flavobacterium*. Their proportion of the total flora increased to 75% by 16 days and 88% by 29 days of storage at 0 C. On the other hand, there was only 23% of Gram-positive, this belonging predominantly to the genera *Micrococcus* and *Corynebacterium*. Some *Actinomyces* were also isolated from control samples (Table III).

TABLE III. Percentage of microbial population of control (unirradiated) sample kept at 0 C.

Genus	1st Day	16 Days	29 Days
Pseudomonas	26	34	40
Achromobacter	13	19	23
Micrococcus	14	9	7
Corynebacterium	9	7	4
Flavobacterium	18	22	25
Actinomyces	12	4	–
Miscellaneous	8	5	1

A great number of Gram-positive chromogenic microorganisms belonging to genera *Micrococcus* were isolated from the samples irradiated at 150,000 rads after 1 day of storage. Their proportion of total population declined considerably after 16 and 29 days of storage. They were supplanted by Gram-negative psychrophilic microorganisms belonging to genera *Pseudomonas*, *Achromobacter*, and *Flavobacterium* (Tavlv IV). As previously mentioned,

TABLE IV. Percentage of microbial population of irradiated samples (using 150,000 rads) kept at 0 C.

Genus	1st Day	16 Days	29 Days
Pseudomonas	1	28	45
Achromobacter	5	14	15
Micrococcus	72	32	10
Corynebacterium	11	4	1
Flavobacterium	5	8	19
Actinomyces	2	6	–
Miscellaneous	4	8	10

some *Actinomyces* isolated in control samples also survived after treatment with 150,000 rads. A few *Staphylococci* colonies were isolated from the 150,000-rad plates, but none were found to be coagulase positive.

As can be seen from Table III, Gram-negative psychrophilic microorganisms dominated the control unirradiated samples throughout the duration of the experiment. Owing to their proteolytic and lipolytic activity, degradation of flesh and abdominal cavity as well as production of yellow pigment were observed after 16 days of storage at 0 C. These changes were not observed in samples treated with 150,000 rads until after 29 days at 0 C. At this time, a significant transition from Gram-positive to Gram-negative organisms had occurred (Table IV). This can be attributed to two important factors, mainly temperature of storage, and proteolytic and lipolytic activities of the *Pseudomonas*. However, at a higher temperature, gram-positives isolated would have also contributed to spoilage of products.

It is interesting to note that the Gram-negative microorganisms isolated from the control unirradiated whitefish were similar to those of Thjotta and Somme (1942) but quantitatively differed slightly to those reported by Evelyn and McDermott (1961). The effect of radiation on the microorganisms isolated supported the findings of Masurovsky et al. (1963) and agreed to some extent to those of MacLean and Welander (1960).

Organoleptic Assessment of Raw Fish

The organoleptic assessment of raw fish showed high initial scores for all samples except those which were exposed to 300,000 rads. These raw samples, after 1 day of storage at 0 C, were characterized by noticeable changes in colour and texture of the flesh, accompanied by a strong "burnt" odour which, after 8 days of storage, gradually disappeared and eventually was replaced by more putrid sour odours. By 16 days the unirradiated whitefish had obvious spoilage odours and softening of flesh, both of which became progressively objectionable during the remainder of the experiment. The control frozen fish, despite slight discolouration of flesh, were judged to be of acceptable quality throughout the experiment. Upon opening the plastic bags after 16 days of storage, some spoilage-like odours were noticed on samples treated with 75,000 and 150,000 rads, which became increasingly evident as the experiment progressed. After 22 days, the flesh of these fish appeared soft and discoloured.

Organoleptic Assessment of Cooked Fish

Panel scores from judgings of cooked whitefish are summarized in Figs. 2 and 3. Because very few judges were present on the 12th day after irradiation, these resuits were omitted.

Composite grade (Fig. 2) represents an overall assessment of each fish made immediately after the individual parameters (Fig. 3) were judged. Of the latter, flavour graphs (Fig. 3) appear the most similar to the composite grades (Fig. 2); hence flavour may be considered to have influenced this generalized opinion strongly.

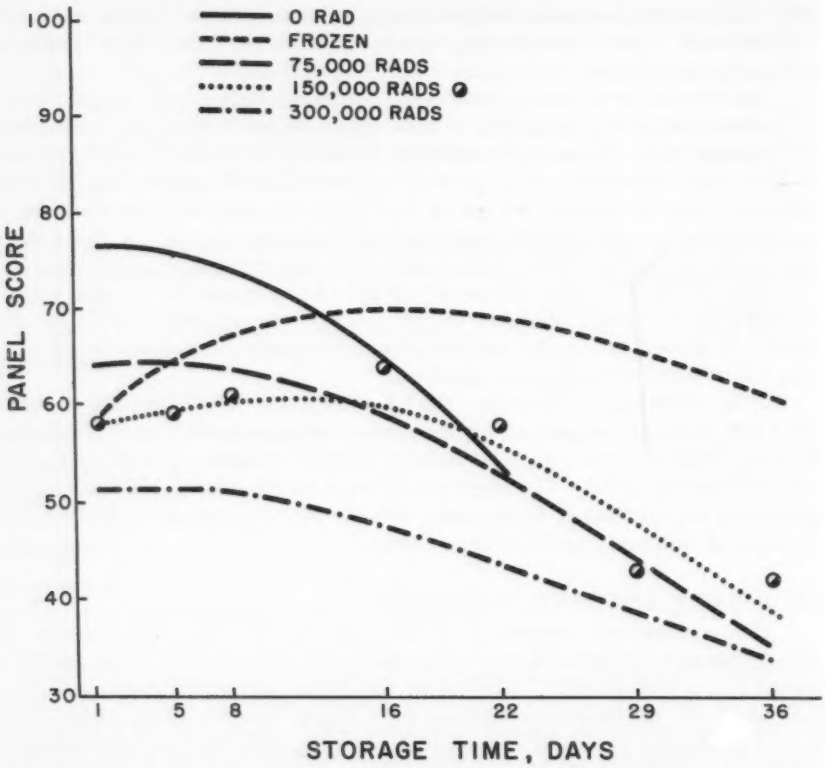

FIG. 2. Composite grade of cooked whitefish by sensory panel. For clarity, points are shown only for the curve of the samples treated with 150,000 rads. A rating below 45 would be unacceptable considering the terms used for grading (Table I). Analysis of variance on data excluding the unirradiated fish showed significant differences ($P = 0.01$) between treatments (error variance 0.739, 133 degrees of freedom) and between days (error variance 2.39, 42 degrees of freedom).

The similarity of the scoring patterns for texture and appearance (Fig. 3) imply that textural changes were obvious. Colour changes were also noted, largely in the irradiated fish, but colour was not scored independently.

With regard to the odour of cooked fish, only the unirradiated fish showed a significant decline over storage (Fig. 3). It should be noted that off-odours apparent in the raw fish volatilized during cooking. Cooked samples were at room temperature when served which also might have minimized odour differences.

For all parameters, the unirradiated whitefish received high initial scores which declined steadily. At 22 days, some judges noted strong unpleasant odours in this cooked fish. For this reason and because the raw fish was considered to

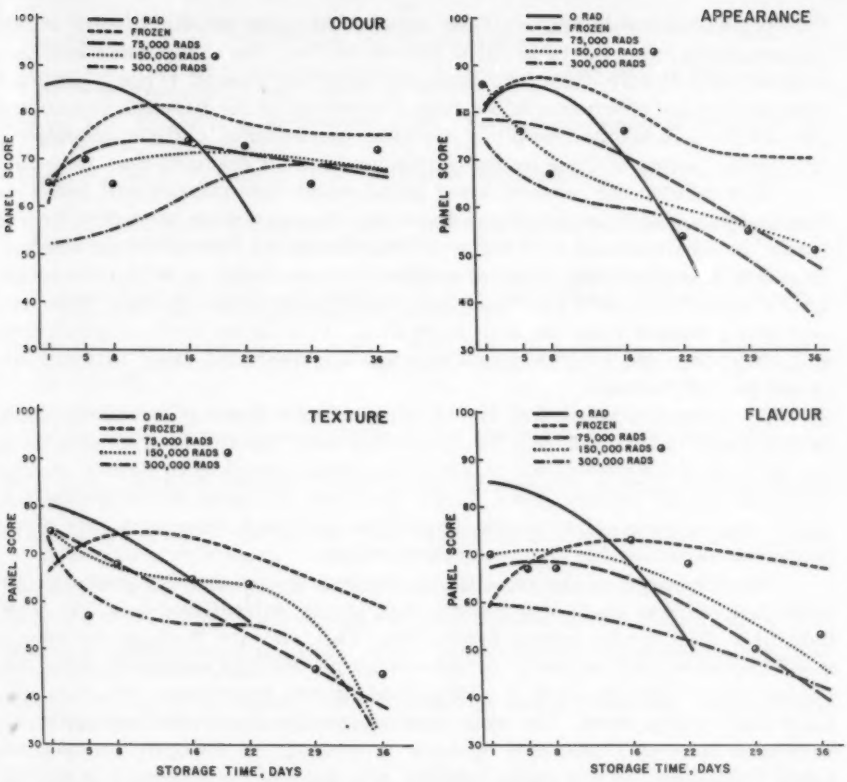

FIG. 3. Panel ratings on odour, appearance, texture, and flavour of cooked whitefish. For clarity, points are shown only for the curve of the samples treated with 150,000 rads. A rating below 45 would be unacceptable considering the terms used for grading (Table I). Analysis of variance on data excluding the unirradiated fish showed significant difference ($P = 0.01$) (a) between treatments in all parameters, with error variance as follows: odour 1.066, appearance 0.746, texture 0.709, flavour 0.836 (137, 132, 132, and 133 degrees of freedom respectively); (b) between days in all parameters except odour, with error variances as follows: appearance 2.108, texture 2.33, flavour 2.164 (each with 42 degrees of freedom).

be unacceptable organoleptically and microbiologically, this fish was excluded from the remaining sensory examinations. Analyses of variance of judges' scores up to 22 days of storage showed significant differences ($P = 0.01$) between treatments in composite grade[3] and in all parameters[4] except texture. Appearance (Fig. 3) was the only parameter showing a highly significant difference ($P = 0.01$) between storage days; this was likely attributable to the sharp decline of the unirradiated sample in this category.

[3]Error variance $\times$ 0.74 with 140 degrees of freedom.
[4]Error variance for flavour, odour, and appearance = 0.9, 1.1, and 0.7 respectively, each with 127 degrees of freedom.

The scores for frozen whitefish showed the same general pattern for all characteristics; that is, the initial score was low but rose to a plateau and then declined only slightly during the remainder of the experiment. It can be assumed that the low initial scores resulted from a tendency of the panelists to compare one sample with another, despite the random presentation, and that the slightly dry, mealy texture of these frozen samples made it less desirable than fresh fish.

All irradiated fish received lower initial scores than unirradiated fish. This was probably due to undesirable odours and flavours; these were described as "stale" in fish irradiated at 75,000 and 150,000 rads and "burnt" in fish irradiated at 300,000 rads. These irradiation effects were no longer noted by the judges after 8 days. All cooked irradiated fish showed some pink colouring under the skin and a tendency for the flesh to be firm. With higher levels of irradiation and with extended storage, discolouration increased and flesh firmness approached "rubberiness".

It may be concluded that of the three different levels of irradiation used in this study, 150,000 rads was found to be the most suitable level for extending the shelf life of fresh whitefish; this fish was acceptable up to 29 days of storage as judged by the sensory panel. Lower levels did not seem to be as effective with a higher proportion of microorganisms surviving whereas higher doses resulted in objectionable changes in the product.

Over the course of the experiment, the decline in composite grades of the irradiated fish was much less marked than in the unirradiated fish, but more noticeable than in the control frozen fish. This and the findings on odour, flavour, texture, and extension of the storage life were in agreement with the results reported by Power et al. (1964; 1964) in the experiment with haddock fillets and scallop meat. The same investigators recommended an optimum irradiation level of 75,000 rads which is in contrast to the optimum level of 150,000 rads found in this study, possibly as a result of the difference in species of fish used.

It must be emphasized that fish used in this experiment were not handled through ordinary commercial channels. Great value might be derived from comparative investigation of storage life of irradiated whitefish when handled under commercial conditions in comparison to this study.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the assistance of Mr B. Kooyman, Director, Fisheries Branch; Mr D. W. Craik, Director, Manitoba Research Council; Dr G. Bligh and Mr A. W. Lantz, Fisheries Research Board of Canada; and the School of Home Economics, University of Manitoba, for the use of their facilities.

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Seasonal Pattern of Return of Atlantic Salmon in the Northwest Miramichi River, New Brunswick[1]

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ABSTRACT

Rates of recapture as grilse of salmon tagged as smolts at two counting fences located 7 and 40 miles above tidehead on the Northwest Miramichi River, New Brunswick, were from 2.5–3.8%. The Northwest Miramichi has early (June–July) and late (September–October) runs of grilse and larger salmon. In this study, returns by and after August 16 are described as early and late respectively. Grilse returns from smolts produced in the headwaters (and tagged at the upper counting fence) were mainly in the early run. Smolts marked at the lower counting fence (but produced in all parts of the river above lower fence) were well represented in both the early and late runs of grilse. Of grilse ascending past the lower counting fence by August 16, a higher percentage of those tagged as smolts at the upper fence than at the lower fence reached the upper part of the river. Of the tagged grilse which ascended past the lower counting fence after August 16, none were recaptured in the upper part of the river. Times of smolt migration to sea and return of grilse appeared to be related to smolt age. Older smolts (age 3 and 4) tended to migrate earlier than younger ones (age 2). Grilse from older smolts were nearly twice as numerous in the early as in the late run; those from younger smolts were nearly equally represented in the early and late runs.

INTRODUCTION

Atlantic salmon, *Salmo salar* Linnaeus, return to eastern Canadian rivers mainly from May through October. In the Northwest Miramichi River there are usually early (mid May to the end of July) and late (mid September to early November) runs which are separated by a period of little salmon movement (August and early Septembe). This situation is illustrated (Fig. 1) by records for 1961 to 1963 of movements past counting fences on the Northwest Miramichi (Henderson et al., MS, 1965). There is a pronounced bimodal pattern for both grilse and larger salmon at the Curventon counting fence which is 7 miles above tidehead, but not at the Camp Adams fence which is 40 miles above tidehead (Fig. 2). The purpose of the present study was to find out if there are distinct early- and late-running stocks of salmon in the Northwest Miramichi or if there is a single stock whose run is interrupted by unfavorable conditions for ascent during August and early September.

Rivers having both early and late runs are usually large and have high rates of discharge at all seasons. There are many small eastern Canadian rivers in which there is only a late run — rivers in which water conditions (discharge and temperature) may be unsuitable for adults to enter during the summer.

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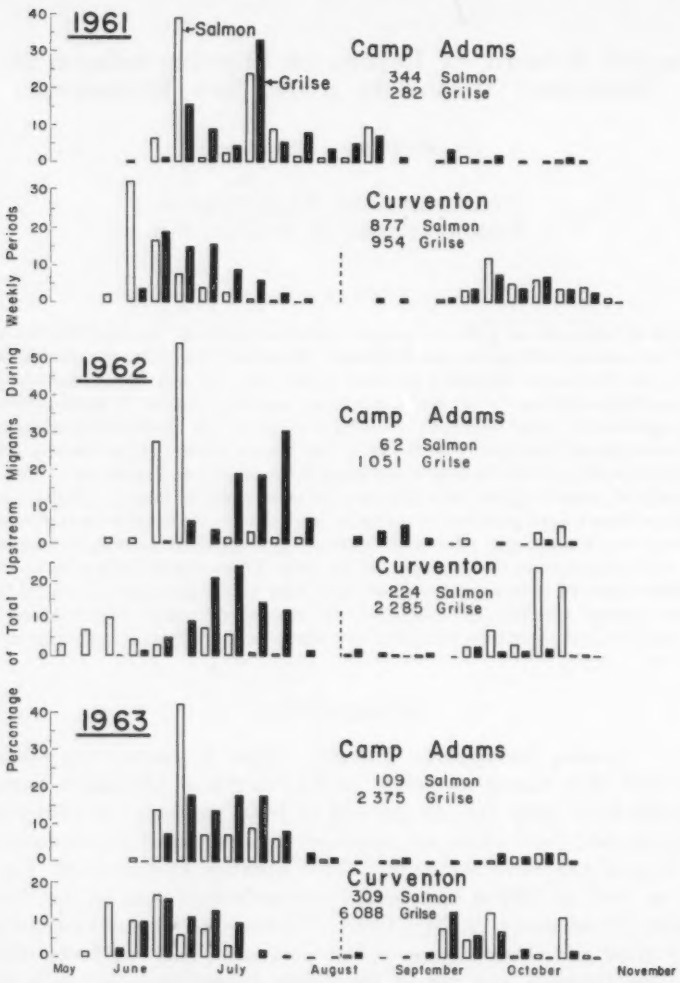

FIG. 1. Temporal patterns of movement of salmon and grilse past two counting fences on the Northwest Miramichi River. Curventon and Camp Adams are respectively 7 and 40 miles above head of tide. Note bimodal pattern at Curventon and single mode at Camp Adams. Broken lines indicate the arbitrary separation of early and late runs at Curventon by and after August 16 respectively.

The questions to be asked are, "Do spring- and fall-run salmon beget spring- and fall-run offspring respectively or do environmental conditions at some time during the river life influence time of return from the sea?" Some experiments with Atlantic salmon have indicated that genetic

factors are of overriding importance (Calderwood, 1930; Zarnecki, 1963); other work supports the thesis that the environment influences season of return (Belding and Kitson, 1934; White and Huntsman, 1938; Sedgwick, 1953).

The early- and late-run phenomenon is of great importance in understanding and managing the Atlantic salmon. Early-run salmon are the most sought after by anglers because they are of better quality and are available in fresh water for more of the angling season. There is a conflict of interests between anglers and commercial fishermen because both exploit the early-run stocks. Late-run fish may contribute substantially to commercial fisheries during certain seasons by being present in coastal waters for some time before running up rivers (Belding and Kitson, 1934; Belding and Préfontaine, 1939) but the relative contribution by early- and late-run salmon has not been determined.

Pacific salmon (*Oncorhynchus*) have been studied with respect to season of return to the river. Experiments involving the planting of hatchery-reared young of known parentage have established that season of return is an inherited characteristic of these fishes and that environmental influences are secondary to genetics in this respect (Rich and Holmes, 1928; Forester, 1946; Donaldson and Allen, 1958; Salo and Bayliff, 1958; Cope and Slater, 1957).

Neave (1949) and Smith (1960) have shown seasonal differences in the time of entry of different stocks of rainbow trout, *Salmo gairdneri*, into British Columbia rivers. Smith (1960) provides convincing evidence that differences in seasonal pattern of return as well as physiological and morphological differences between two stocks of rainbow trout in Capilano River, B.C. are under hereditary control.

METHODS

Fish used in this study were smolts naturally produced in the Northwest Miramichi River, N.B. They were collected during May–June smolt runs at the Curventon and Camp Adams counting fences (Fig. 2).

In 1960, 750 smolts captured at Camp Adams between May 25 and 30 were marked with numbered tags like the Swedish smolt tag (Carlin, 1955). No smolts were marked at Curventon in 1960.

In 1962, 1582 smolts were tagged at Camp Adams and an additional 1978 were marked by removing the adipose and left pelvic fins. At Curventon, 4030 smolts were tagged and 14,120 were fin-clipped (adipose and left pelvic fins). Smolts captured at Camp Adams came from the headwaters; smolts captured at Curventon were a mixture of those which missed being captured at Camp Adams and those coming from tributary rivers and the main stem Northwest Miramichi between the two counting fences.

The same fin-clip combination was used at both fences so it was not possible to distinguish among returning fin-clipped adults those marked at one site or the other. Data associated with returning fin-clipped grilse are considered only in the discussion of smolt age in relation to time of grilse return.

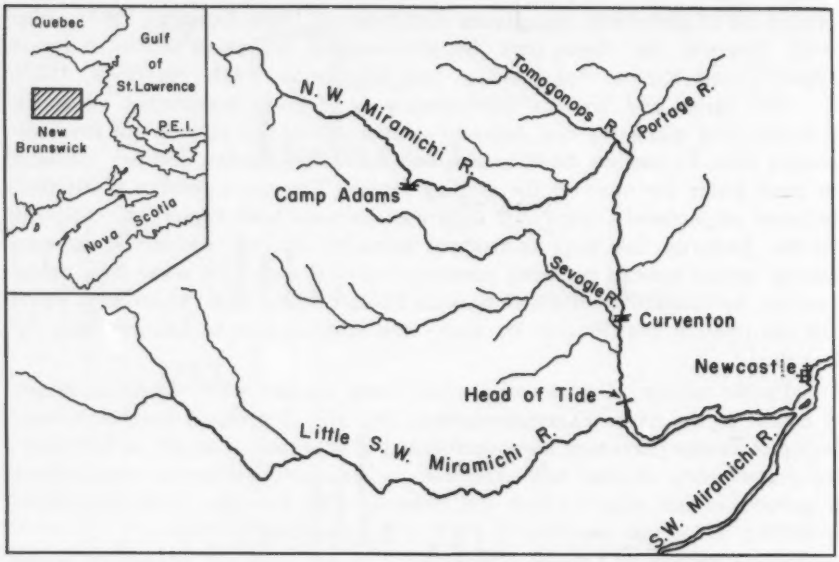

FIG. 2. Northwest Miramichi River system showing locations of counting fences and tributaries.

Figure 3 shows when fish were tagged during the 1962 smolt runs at Camp Adams and Curventon. Mean lengths of three samples of smolts taken at various times during the Camp Adams run suggested a slight decrease in smolt length during the run.

Recoveries of tagged adults were made in the angling and commercial fisheries and at the Curventon and Camp Adams counting fences. A reward of $1.00 per tag encouraged fishermen to report captures of tagged fish. Technicians of the Fisheries Research Board made regular visits to angling and commercial fishing centers in the Miramichi area to collect recapture data. Distant recaptures were reported through protection officers of the Department of Fisheries of Canada or directly by mail. Many recaptures were made at the counting fences which were operated annually during the open-water season. It is felt that few, if any, of the salmon ascending past Curventon escaped notice at either counting fence. Only one tagged grilse was recaptured at Camp Adams without first having been seen at Curventon. Of the fish that returned to the Northwest Miramichi but did not ascend past Curventon fence, only those angled are considered here.

Anglers and commercial fishermen were encouraged to supply the following information: tag number, place and date of capture, length and weight of specimen, and a sample of scales. Data pertaining to length and weight and scale samples were often lacking, particularly from distant recaptures. The most useful data were obtained at the counting fences where careful attention was paid to returning tagged fish.

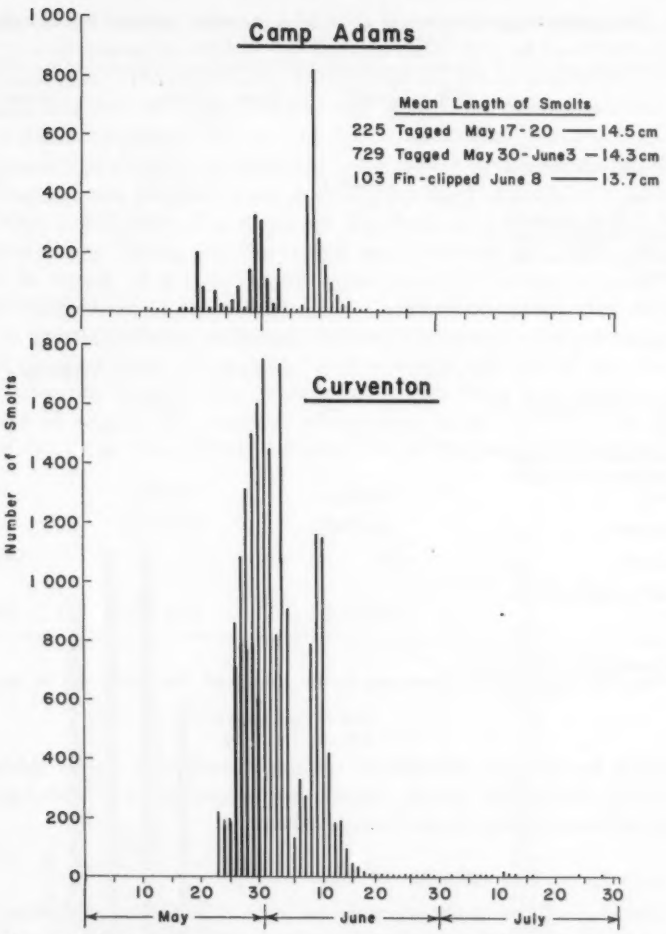

FIG. 3. Seasonal patterns of smolt descent past Camp Adams and Curventon in 1962. Numbers of fish tagged and fin-clipped on particular days are indicated by the thick and thinner lines respectively. Mean lengths are given for three samples of smolts collected at Camp Adams.

Considerations of early and late return deal only with grilse because recaptures of 2-sea-year salmon in fresh water were too few to give an adequate basis for study. In this study, returns by and after August 16 are described as early and late respectively.

RESULTS AND DISCUSSION

Total recaptures as grilse were from 2.5–3.8% among the three groups of tagged fish (Table I). Total recaptures are separated into freshwater (angling

TABLE I. Recaptures in various areas as grilse from naturally produced smolts tagged in the Northwest Miramichi River.

	Camp Adams[a] 1960	Camp Adams 1962	Curventon 1962
Recaptures in commercial fishery	6(32%)	5(8%)	24(23%)
Recaptures in fresh water of Northwest Miramichi system (angling and counting fences)[b]			
By Aug. 16	13(100%)	43(81%)	46(60%)
After Aug. 16	0(0%)	10(19%)	31(40%)
Total	13(100%)	53(100%)	77(100%)
Recaptures In other rivers (angling)	0	2	1
Total recaptures in fresh water (angling and counting fences)	13(68%)	55(92%)	78(77%)
Total recaptures	19(100%)	60(100%)	102(100%)
Number tagged	750	1582	4030
Number and percentage recaptures	19(2.5%)	60(3.8%)	102(2.5%)

[a]Place and year of tagging.
[b]Includes fish angled below Curventon in the Northwest Miramichi and in the Sevogle River.

and counting fence) and commercial catches. Recaptures above tidehead in the Northwest Miramichi system include fish angled below Curventon in the Northwest Miramichi and in the Sevogle River.

EARLY- AND LATE-RUN GRILSE

The findings of this study strongly indicate that there are distinct early- and late-running stocks of Atlantic salmon in the Northwest Miramichi rather than a single stock whose run is interrupted by unfavorable conditions for ascent during August and early September.

All 13 grilse recaptured in fresh water of the Northwest Miramichi in 1961 (from smolt tagging at Camp Adams in 1960) were in the early run and in fact before July 26 (Table I). Although 67% of the 1961 grilse run had passed Curventon by this time, such a pattern of early return by the 13 grilse was probably not a chance result ($p < 0.01$).

The 1963 returns of tagged grilse (1962 smolt-class[2]) added more data on the seasonal pattern of return to the river. Of 53 grilse tagged as smolts at

[2]A smolt-class consists of all salmon which became smolts during a calendar year, regardless of their year-class.

Camp Adams and caught above tidehead in the Northwest Miramichi system, 43 or 81% were taken by August 16. By this time, 65% of the 1963 grilse run had ascended past Curventon fence. Of 77 grilse tagged as smolts at Curventon and caught as grilse above tidehead in the Northwest Miramichi, only 46 or 60% were taken by August 16.

Temporal distributions in return of grilse tagged as smolts at Camp Adams and Curventon were analysed more critically by the Kolmogorov–Smirnov test (Siegel, 1956, p. 127–136). The temporal distributions of returning grilse tagged as smolts at Camp Adams and Curventon were different ($p < 0.01$). Moreover, the time of return of Camp Adams grilse to the Curventon area differed ($p < 0.01$) from that of the total run at Curventon (tagged plus untagged). There was not a significant difference between the temporal distribution of the combined tagged Camp Adams and Curventon fish and that of the total grilse run at Curventon (tagged plus untagged), so that there is no reason why the two groups of tagged fish together should not be taken as a representative sample of the grilse run. Figure 4 shows the comparison between times of re-

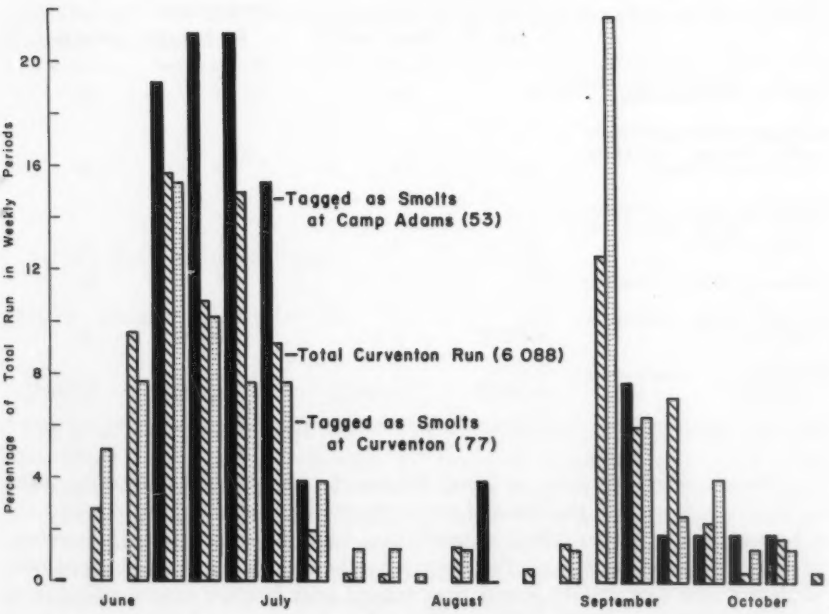

FIG. 4. Percentage returns to Northwest Miramichi during weekly periods in 1963 of grilse which had been tagged as smolts at Curventon and Camp Adams in 1962. Returns of fish tagged at Curventon and Camp Adams are compared with the total (tagged plus untagged) run of grilse at Curventon. Note predominance of returns of Camp Adams fish in June and July, and distribution of Curventon grilse in early and late runs in closer resemblance to that of total run. Numbers of grilse in each category are indicated in brackets.

turn of grilse tagged as smolts at Camp Adams and Curventon. Thus, smolts produced in the headwaters give rise mainly to early returning grilse.

Do Grilse Return to the Level of the River in Which They Lived as Parr?

Of the early-run grilse which ascended and stayed above[3] Curventon in 1963 and were not recaptured in intermediate levels of the river, a higher percentage of those tagged as smolts at Camp Adams (70%) than of those tagged at Curventon (53%) reached the Camp Adams area (Table II). Of those ascending past Curventon after August 16, none were recaptured at the Camp Adams fence or were angled in the upper part of the river.

Table II. Fates of early- and late-run grilse, tagged as smolts at two counting fences in 1962, which ascended past Curventon in 1963. Percentages given are of the number remaining after subtracting fish angled in intermediate stretches and those lost because of pollution.

	Camp Adams ascended		Curventon ascended	
	By Aug. 16	After Aug. 16	By Aug. 16	After Aug. 16
Total number ascending	40	10	41	29
Angled in intermediate stretches between Curventon and Camp Adams	2	0	2	0
Descended past Curventon fence during periods of high pollution	1	2	1	6
Remained above Curventon	37	8	38	23
Reached Camp Adams or vicinity	26(70%)	0	20(53%)	0
Remained in intermediate stretches	11(30%)	8(100%)	18(47%)	23(100%)

Ascent as far upstream as Camp Adams of early- but not of late-run grilse might be explained on the basis of return to the level of the river in which the fish were reared. Carter (1963) suggests that adult Atlantic salmon may return to the particular portion of the river wherein they were stocked as smolts. Saunders and Gee (1964) found that tagged parr have a strong affinity for particular small areas (their "homes") within a stream and that some return to these "homes" after having been experimentally displaced as far as 700 ft up river or downriver. Hence, salmon returning from the sea may retain a

[3]Copper and zinc pollution from a base metal mine on a tributary resulted in some fallback of salmon which had ascended past Curventon counting fence (Sprague et al., 1965).

familiarity with a local area of a stream in which they lived as parr and the ability to return to such an area. Smolts tagged at Camp Adams had presumably been produced above that point. Those tagged at Curventon had come from all parts of the river above Curventon: some undoubtedly were produced above Camp Adams and escaped capture at the upper fence. The latter could have contributed substantially to the early-run grilse which had been tagged as smolts at Curventon. A possible explanation for the lower percentage of early-run Curventon grilse (tagged as smolts) than of Camp Adams grilse reaching Camp Adams is that the area for some miles below Camp Adams produced smolts which became early-run grilse. If these on returning did not ascend far above the areas in which they lived as parr, this could account for the different percentages of early-run grilse which reached the Camp Adams area.

Relation Between Smolt Age and Time of Return as Grilse

Smolt ages were read from scales collected from 689 returning grilse at Curventon fence during 1963. These fish had been tagged or fin-clipped as smolts in 1962 at Camp Adams and Curventon and were therefore known to have been produced in the Northwest Miramichi. The numbers of grilse in the early and late runs that had been tagged or fin-clipped as smolts at the various ages were as follows.

	Smolt age (*years*)		
	2	3	4
Early run (June 12–August 16)	153	229	15
Late run (August 17–October 24)	156	134	2
Totals	309	363	17

Grilse from age-2 smolts were nearly equally represented in the early and late runs, those from age-3 smolts were 1.7 times as numerous, and grilse from age-4 smolts were 7.5 times as numerous in the early as in the late run. Since the sample of grilse from age-4 smolts is small, these are considered with the age 3's. Grilse from 3- and 4-year smolts combined were 1.8 times as numerous in the early as in the late run. Thus, there is a clear tendency for grilse from older smolts (ages 3 and 4) to return in the early run.

Table III is a further analysis of the data in the text table. Numbers of tagged and fin-clipped grilse are given separately for early and late runs according to smolt age. Data for tagged fish are separated according to place where smolts were tagged. Age-3 and -4 smolts are combined because age 4's were too few to be considered separately.

Figure 3 shows that tagging in 1962 was done near the beginning of the smolt run at both counting fences. Although fin-clipping was done throughout the runs, the bulk of it was done later than the tagging. Accordingly, for comparison, the tagged fish are considered as early- and the fin-clipped fish as late-migrating smolts. Table III and the above consideration show the following. Among early migrating smolts the ratio of younger (age 2) to older (ages 3 and 4) smolts was 1:3. Among late-migrating smolts the ratio was 1:1. Summarizing, it appears that older smolts tend to migrate to sea earlier than younger ones and that older smolts are more likely to return as early-run grilse than are younger smolts.

TABLE III. Numbers of grilse in early and late runs at Curventon in 1963 according to place where smolts were tagged and to age of the smolts when tagged (early migrating) or fin-clipped (late migrating).

	Smolt age								
	Tagged grilse			Fin-clipped grilse			Total		
	2	3+4	Total	2	3+4	Total	2	3+4	Total
Early run									
Camp Adams	8	29	37	–	–	–	–	–	–
Curventon	11	29	40	–	–	–	–	–	–
Total	19	58	77	134	186	320	153	244	397
Late run									
Camp Adams	4	5	9	–	–	–	–	–	–
Curventon	5	20	25	–	–	–	–	–	–
Total	9	25	34	147	111	258	156	136	292
Total early and late									
Camp Adams	12	34	46	–	–	–	–	–	–
Curventon	16	49	65	–	–	–	–	–	–
Grand total	28	83	111	281	297	578	309	380	689

Sedgwick (1953) read the smolt ages from scales of large salmon and grilse entering the Miramichi system in 1950 and found that fish of low smolt age (2 year) were scarce in the early run and common in the late run. Blair (1935) noted, in samples of adult salmon taken in the Miramichi commercial fishery, a similar although slight increase in the number of 2-year smolts and a corresponding decrease in the number of older (3- and 4-year) smolts as the 1931 fishing season progressed. Although Sedgwick's and Blair's findings are in

agreement with the present work, the samples were not strictly comparable. In the present work, all of the grilse originated as smolts from the Northwest Miramichi whereas some of Sedgwick's fish were taken in the estuary of the Northwest Miramichi and could have been produced in the Little Southwest or even the Southwest Miramichi River. Salmon in Blair's samples from the commercial fishery in the common Miramichi estuary and the drift-net fishery in Northumberland Strait could have been produced in any of a number of rivers other than the Northwest Miramichi.

Sedgwick suggested that early- and late-run salmon may utilize different spawning areas in the same river and that these areas may differ sufficiently in environment to influence the growth rates of young salmon living in them. The present study shows that many early-run grilse reached the Camp Adams area whereas late-run fish did not (Table II). Figure 1 shows for 3 years that few of the salmon arriving at Curventon during September and October ascend as far as Camp Adams. There are differences in water temperature between Camp Adams and Curventon. The former is consistently cooler during the season of counting fence operation. However, water temperatures at Curventon seldom if ever exceed tolerable levels for continued parr existence. Unfortunately, there are no comparative data on the relative abundance of food organisms in the upper and lower levels of the river.

ACKNOWLEDGMENTS

I am grateful to Dr C. J. Kerswill under whose guidance the Miramichi smolt sampling and adult salmon trapping facilities were developed. Dr M. H. A. Keenleyside started the smolt tagging program on the Miramichi. Recaptures from his tagging at Camp Adams in 1960 gave the leads which stimulated the work reported in this paper. The following assisted in one way or another during smolt trapping and tagging, and capture of returning adult fish: Dr and Mrs John H. Gee and Messrs E. J. Schofield, I. M. Jones, W. G. Irving, E. A. J. Chambers, R. J. Gibson, E. C. Tucker, R. H. Currie, and W. R. Currie. Drs M. W. Smith, P. F. Elson, and D. G. Wilder and Messrs K. R. Allen and M. L. H. Thomas offered helpful suggestions during the preparation of this paper. Miss Marion Haley catalogued the tag recapture data, Mr C. D. Grant determined smolt ages of recaptured tagged and fin-clipped grilse, and Mr P. W. G. McMullon prepared the illustrations.

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Vertical Distributions of Some Benthic Marine Algae in a British Columbia Inlet, as Related to Some Environmental Factors[1]

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ABSTRACT

The vertical distribution of 12 benthic marine algae and one animal are described for Indian Arm, an inlet in British Columbia. In general, the vertical distributions had distinct limits and the relative vertical positions of the species were constant throughout the inlet. The relative vertical distributions of the biota within the inlet are essentially the same as described for the northeast Pacific by other authors concerned with the same biotic elements. However, the upper limits of *Laminaria saccharina* (L.) Lamouroux, *Costaria costata* (Turn.) Saunders, and *Constantinea subulifera* Setchell are from 1 to 3 m lower within the inlet than elsewhere, whereas those of *Agarum cribosum* Bory, *Fucus evanescens* C. Agardh, and *Sargassum muticum* (Yendo) Fensholt are essentially the same within and outside of the inlet. For the remaining species studied (*Enteromorpha compressa* (L.) Greville, *E. linza* (L.) J. Agardh, *E. intestinalis* (L.) Link, *Monostroma fuscum* (Postels & Ruprecht) Wittrock, *Ulva lactuca* Linnaeus, *Navicula grevillei* (C. Ag.) Cleve, and *Balanus glandulus* (Darwin)) there were no comparable distribution data outside of the inlet.

Available data suggest the deepening of the upper limits of some algae in Indian Arm reflects their intolerance to the high temperature and low salinity of the surface waters of the inlet.

INTRODUCTION

The purpose of the present study was to define the vertical distributions of some conspicuous benthic marine algae over an extended horizontal range in an area having well-defined environmental parameters, and to compare these distributions with those described by earlier workers who were concerned with similar floras in the northeast Pacific.

Numerous descriptions of marine algal distributions are available for the northeast Pacific. Studies comparing vertical profiles of algal distributions have been published by Doty (1946) for the northeast Pacific; by Rigg and Miller (1949) for the Neah Bay region, Washington; by Scagel (1961) for Queen Charlotte Strait, British Columbia; by Stephenson and Stephenson (1961, 1961a) for the southern end of Vancouver Island, British Columbia; by Neushul (1965) for San Juan Island, Washington; and by Widdowson (1965) for 34 stations along the northern shore of Juan de Fuca Strait, British Columbia. These authors related the observed differences in zonation to tidal

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factors, surf action, directional orientation of the substratum, and vertical distributions of temperature, salinity, and light.

Of the above cited contributions only those of Neushul (1965) treated subtidal distributions comprehensively.

AREA OF STUDY

Indian Arm, an extension of Burrard Inlet, Vancouver, British Columbia, is a long (22 km), narrow (0.5–2.5 km) inlet, longitudinally oriented north to south (Fig. 1). The west and east sides of the inlet are bordered by steep mountains. The substratum of the benthic zone is nearly vertical cliffs, dissected irregularly by outwash fans of rubble originating from steep ravines. The region selected for study extends from a point 2 km south of the inlet head for 13 km along the eastern wall.

METHODS

Measurements of vertical distributions were made by observers using scuba gear from August 8–15, 1964 at 10 shore stations along the eastern side of Indian Arm. The stations selected had uniform western exposures and nearly vertical profiles.

Bench marks were placed at each station near the high-water level. The positions of the 10 bench marks relative to various tide levels were ound by measuring the distances between the bench marks and the water surface and then relating these measurements to the tidal heights predicted for the Buntzen Power Station (Canadian Hydrographic Service, Department of Mines and Technical Surveys, 1963) at the time of measurement. This procedure was performed several times at each bench mark.

The general procedure for determining the vertical limits of the algae studied was as follows. Upon entering the water, a scuba diver surveyed the benthic zone for a distance of approximately 10 m on either side of the bench mark. During this phase of the study the diver made general observations and collected voucher specimens. When acquainted with the station, the diver measured the vertical limits of the algae in question. The limits of the submerged algae in relation to the surface were determined by the diver by using a steel tape measure suspended from a buoy. After orienting the tape to the position to be measured, the diver would attach a weight to the tape and allow the tape to assume a plumb-line position. The distance from plant to surface was added to the surface-to-bench-mark measurement. The vertical limits of the exposed algae were determined by measuring from the plants to the bench mark. All measurements made above the water surface were made with a rigid 2-m rule. The absence of appreciable surface disturbances during the time of measurement permitted reliable results.

The temperature, salinity, and density data employed in this study were obtained from five stations (Fig. 1) in Indian Arm (Institute of Oceanography, University of British Columbia, 1958, 1959, 1960, 1963, 1964). Isopleths of

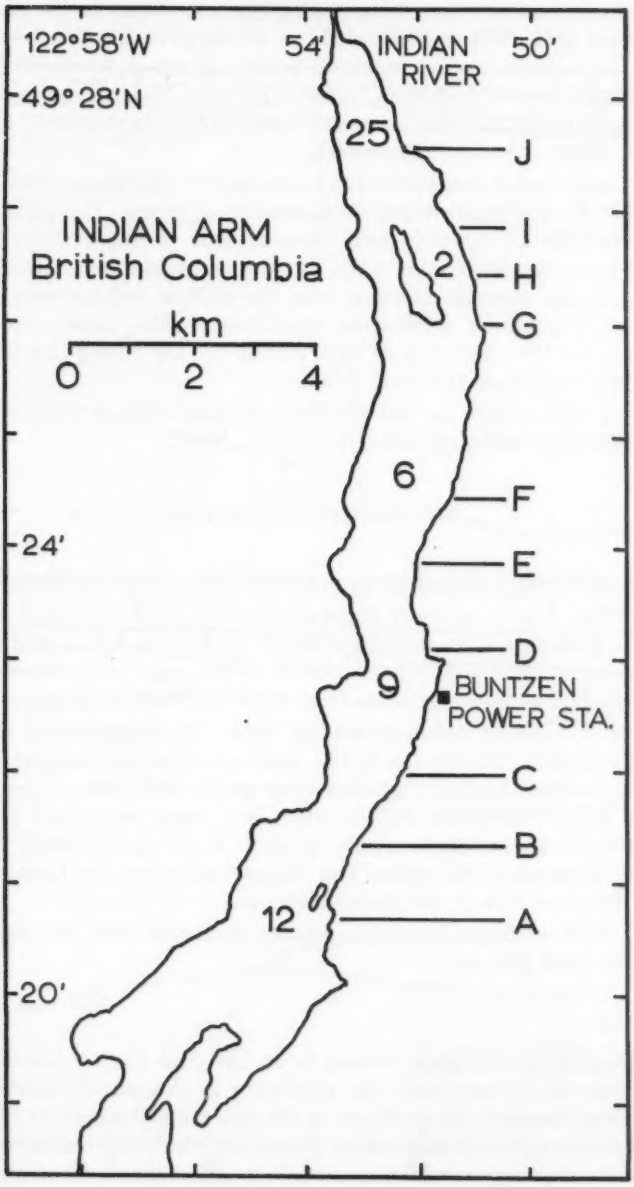

FIG. 1. Geographical features of Indian Arm. The numbers (12, 9, 6, 2, 25) indicate oceanographic stations. The letters (A–J) indicate stations of the algal survey.

temperature and salinity were determined from mean values for 3-month periods for the years 1957–1959 and 1962–1963 at depths of 0, 2.5, 5.0, 7.5, 10.0, and 20.0 m. The 3-month periods relate to periods of runoff as described by Gilmartin (1962): winter minimum runoff (January–March), spring maximum runoff (April–June), summer minimum runoff (July–September), and winter maximum runoff (October–December).

Light attenuation coefficients were provided by Buchanan (1966) for 4500 Å and 6500 Å wavelengths using a transmittance meter. The light data employed were collected monthly from October 1962 to August 1963 except for May and June. Readings were taken at each oceanographic station indicated in Fig. 1 at 1-m intervals starting from the surface and proceeding to 5 m depth. The attenuation coefficients presented in this paper represent the mean values for the upper 5 m at each station for the period October 1962 to August 1963 (excepting May and June).

Further information on the physical oceanography of Indian Arm was derived from the studies of Gilmartin (1962, 1964).

ENVIRONMENTAL FACTORS

Salinity

Gilmartin (1962) describes the vertical distribution of salinity for the head of Indian Arm in terms of three strata: a brackish surface layer 1.5–2.5 m thick, a transition layer ranging in depth from 2.5 to 5.0 m, and a bottom layer of more saline water. The thickness of the upper two strata decreases while the surface salinity increases from the inlet head to mouth.

Figures 2–3 depict isohalines for the upper 15 m throughout the section of the inlet studied. During the spring maximum and the summer minimum runoffs the horizontal salinity gradients are greatest. During the winter minimum and winter maximum runoffs there is a small horizontal gradient of surface salinity. The vertical salinity gradient is of approximately the same magnitude throughout the year. The highest salinities are found near the mouth of the inlet and in the deeper waters.

The annual variation in surface salinity decreases from the head to the mouth of the inlet (Fig. 4).

Temperature

Temperature of the upper waters in Indian Arm has an annual cycle of one minimum in January and one maximum in August (Gilmartin, 1962). The horizontal temperature gradients in the area studied are slight (Figs. 2–3). A vertical temperature gradient exists throughout the year. During the spring maximum and the summer minimum runoffs the warmer water is at the surface, whereas during the winter maximum and winter minimum runoffs the colder water is at the surface. The annual variations in surface temperature are similar for all stations (Fig. 4).

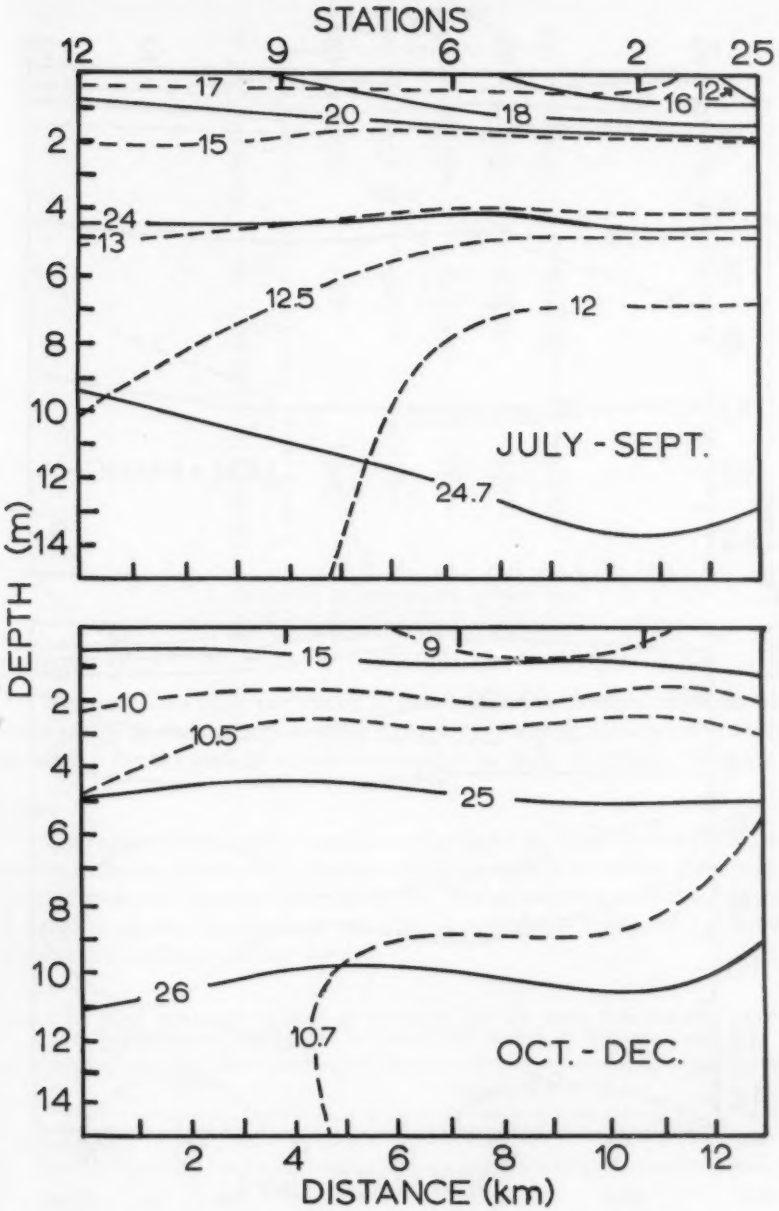

FIG. 2. Isotherms of mean temperature (C (broken line)) and isohalines of mean salinity (‰ (solid line)) in Indian Arm for the periods January–March and April–June, 1957–1959, 1962–1963.

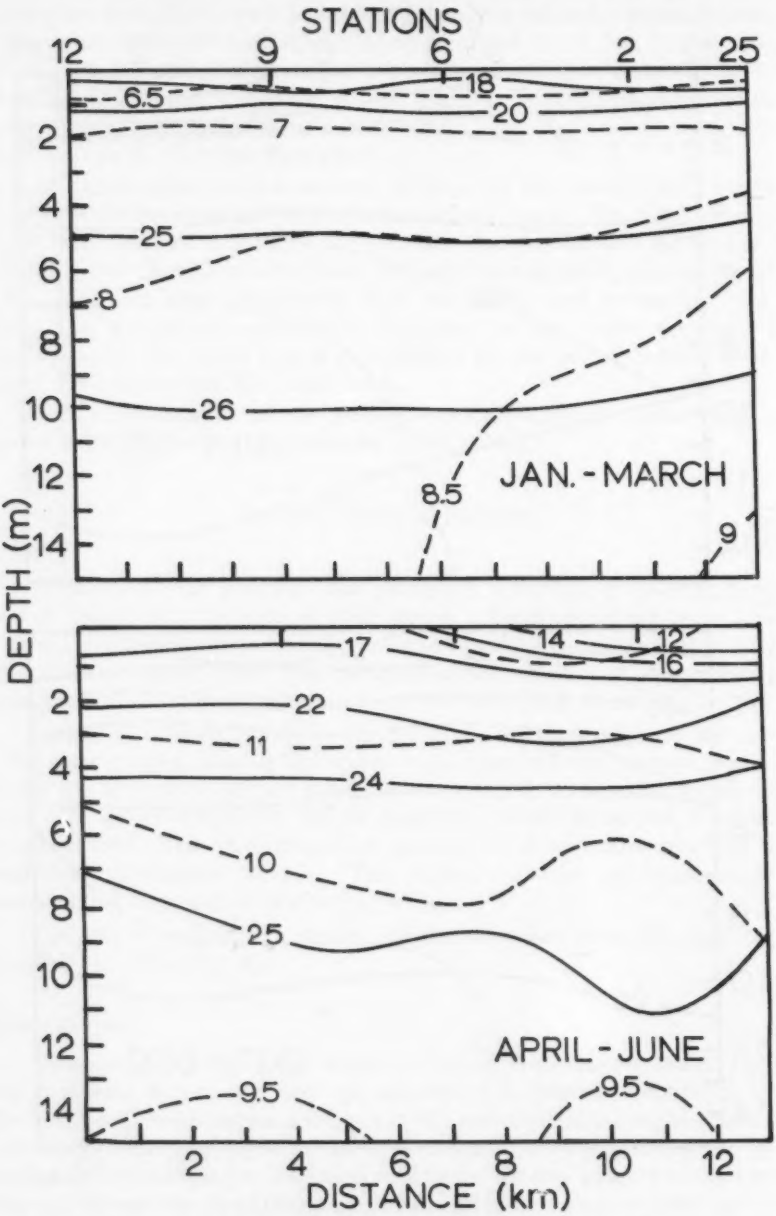

FIG. 3. Isotherms of mean temperature (C (broken line)) and isohalines of mean salinity (‰ (solid line)) in Indian Arm for the periods July–September and October–December, 1957–1959, 1962–1963.

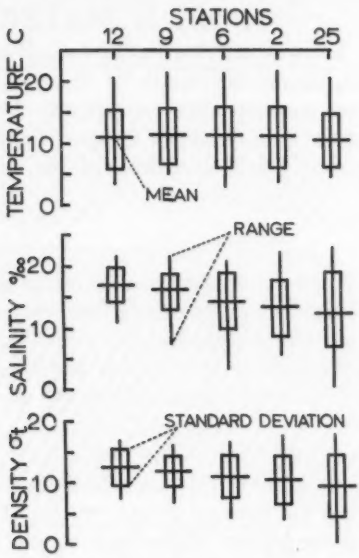

FIG. 4. Ranges, means, and standard deviations of temperature, salinity, and density of surface water in Indian Arm for the periods 1957–1959, 1962–1963.

DENSITY

Because of the large variations in salinity relative to those of temperature, the isopleths of density follow those of salinity. Further, the annual variations of density for the surface waters are similar to those of salinity (Fig. 4).

LIGHT

The mean attenuation coefficients for light at 4500 and 6500 Å wavelengths indicate a horizontal gradient of this property in Indian Arm with the clearest water at the inlet head (Table I). The penetration of light in the 6500 Å range is greater than that of the 4500 Å range as is indicated by the lower attenuation coefficient of the former.

TABLE I. Mean attenuation coefficients determined for the upper 5 m through Indian Arm for the period October 1962 to August 1963 (except for May and June).

	Station				
Wavelength	12	9	6	2	25
4500 Å	0.96	0.96	0.88	0.86	0.87
6500 Å	0.81	0.76	0.68	0.68	0.68

Nutrients

The only data on nutrient distribution in Indian Arm are those for phosphate–phosphorus taken during the month of March 1959 (Gilmartin, 1962). At this time the surface concentration was slightly higher at the inlet head (1.84 μg-at P/liter) than at the mouth (1.49 μg-at P/liter). The concentration at 30 m was approximately 2.5 μg-at P/liter at the inlet head and 2.1 μg-at P/liter at the mouth.

Oxygen

Gilmartin (1962) noted an oxygen concentration increase in the surface waters from the inlet head to mouth during the winter and a decrease from the head to mouth in summer. Values ranging from 5 to 9 mg oxygen/liter are typical for all stations throughout the year at the 2.5–5.0 m depths. Surface conditions are more variable, with concentrations as high as 15 mg oxygen/liter.

Tides

The tides in Indian Arm are of the mixed semidiurnal type. The predicted maximum tidal amplitude for Buntzen Power Station (Fig. 1) is 4.8 m (16 ft). The relative positions of the highest higher high water (HHHW), mean of the high waters (MHW), mean sea level (MSL), mean of the low waters (MLW), and the lowest lower low water (LLLW) are illustrated in Figs. 5–7.

RESULTS

The vertical distributions of 12 algae and one animal (Table II) were determined. In some cases it was not possible to determine both the upper and lower limits accurately. This was due to similarity in life-forms of two species growing together or in juxtaposition.

In general the vertical distributions throughout the inlet had distinct limits (Figs. 5–7). Further, the relative vertical positions of the species did not change. These distributional relationships were better defined with the perennial species than with the ephemeral species (Table II, Figs. 5–7).

The distributions of the lower limits of *Laminaria saccharina* and the upper limits of *Agarum cribrosum* constitute an exception to the general distribution pattern described above. Their vertical limits were closely placed with little overlapping at stations A–F (Fig. 5). At stations F–J there was progressively more overlapping of these two species.

The upper limits of *Balanus glandulus* and *Fucus evanescens* were closely positioned at stations A–H. At stations I and J the upper limits of *F. evanescens* were approximately 1 m below those of *B. glandulus*.

Five members of the Ulvales were encountered (Fig. 6). Because of the frequent overlapping of species having similar life-forms it was possible to determine only the lower limits of *Enteromorpha linza* and *Monostroma fuscum* and the upper limits of *Ulva lactuca* with any degree of certainty. *Enteromorpha*

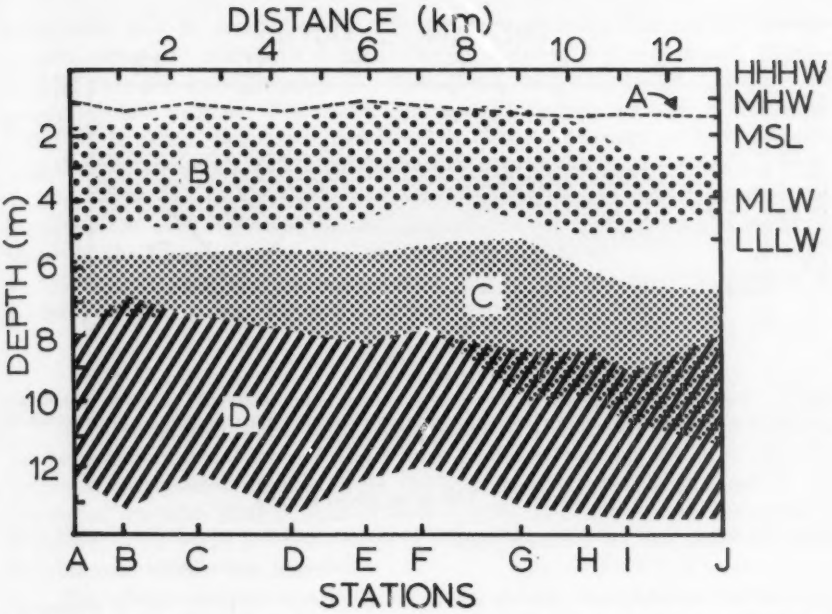

FIG. 5. Observed distributions of *Balanus glandulus*, upper limits (A), *Fucus evanescens* (B), *Laminaria saccharina* (C), and *Agarum cribrosum* (D). HHHW (highest higher high water), MHW (mean high water), MSL (mean sea level), MLW (mean low water), LLLW (lowest lower low water).

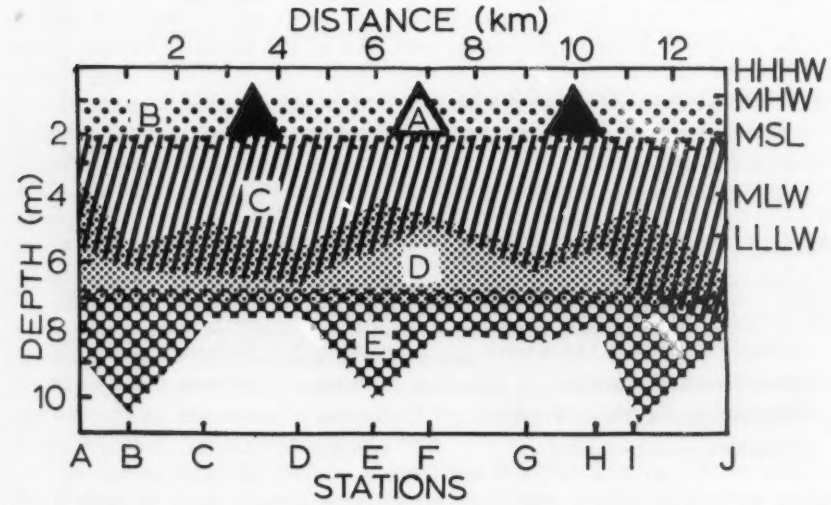

FIG. 6. A schematic presentation of the distributions of *Enteromarpha compressa* (A), *E. intestinalis* (B), *E. linza* (C), *Ulva lactuca* (D), and *Monostroma fuscum* (E). The upper limits of *U. lactuca* and the lower limits of *M. fuscum* and *E. linza* represent detailed measurement; the remaining limits are approximations. See Fig. 5 for explanation of tidal heights.

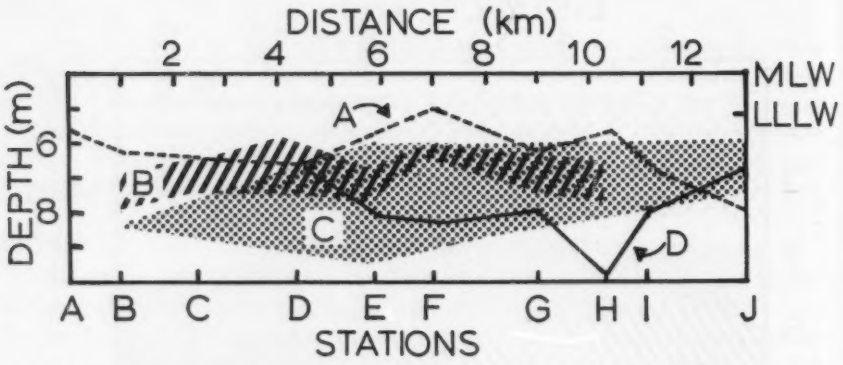

FIG. 7. Observed distributions of *Enteromorpha linza*, lower limits (A), *Costaria costata* (B), *Contantinea subulifera* (C), and *Navicula grevillei*, lower limits (D). See Fig. 5 for explanation of tidal heights.

TABLE II. List of organisms studied.

Species	Accuracy of vertical limits		Number of stations
	Upper	Lower	
Ephemeral species:			
Enteromorpha linza (L.) J. Agardh	Approximate	Accurate	9
Enteromorpha compressa (L.) Greville	Approximate	Approximate	3
Enteromorpha intestinalis (L.) Link	Approximate	Approximate	10
Monostroma fuscum (Postels & Ruprecht) Wittrock	Approximate	Accurate	10
Ulva lactuca Linnaeus	Accurate	Approximate	9
Navicula grevillei (C.Ag.) Cleve	–	Accurate	7
Perennial species:			
Agarum cribrosum Bory	Accurate	Accurate	10
Costaria costata (Turn.) Saunders	Accurate	Accurate	7
Laminaria saccharina (L.) Lamouroux	Accurate	Accurate	10
Fucus evanescens C. Agardh	Accurate	Accurate	10
Sargassum muticum (Yendo) Fensholt	Accurate	Accurate	3
Constantinea subulifera Setchell	Accurate	Accurate	3
Animal species:			
Balanus glandulus (Darwin)	Accurate	–	10

intestinalis and *E. compressa* inhabited the upper intertidal region. *Enteromorpha compressa* was most conspicuous in regions of direct runoff. *Enteromorpha linza* was immediately below these two forms in the lower intertidal and upper subtidal regions. The upper limits of *U. lactuca* were near the lower limits of *E. linza*. The lower limits of *U. lactuca* extended to 1–2 m below LLLW, where this species was replaced by *M. fuscum*.

Although the lower limits of the colonial diatom *Navicula* (*Schizonema*) *grevillei* were very irregular they were of interest since they formed a mirror image of the lower limits of *E. linza* (Fig. 7).

Sargassum muticum, introduced from Japan, was observed at stations A, C, and E, where it was restricted to just below the LLLW.

DISCUSSION

As already mentioned, light attenuation in the upper 5 m and salinity are two environmental factors which form gradients through the inlet. Salinity and light attenuation increase from the inlet head to outh. Because of the somewhat irregular distributions of some species, it is not possible to advance a general hypothesis for the effects of these gradients on the observed algal distributions within the inlet.

The relative vertical distributions of the marine organisms in Indian Arm are essentially the same as those described for the northeast Pacific by earlier workers concerned with the same biotic elements (Muenscher, 1915; Rigg and Milier, 1949: Scagel, 1961; Stephenson and Stephenson, 1961, 1961a; Neushul, 1965; Widdowson, 1965). However, the vertical limits of the benthic algae in Indian Arm differ from those recorded by these earlier workers in that the upper vertical limits of the Indian Arm plants are, in some instances, appreciably lower.

In areas studied outside of Indian Arm the upper limits of *L. saccharina*, *Costaria costata*, and *Constantinea subulifera* are found between MLW and LLLW (Muenscher, 1915; Rigg and Miller, 1949; Scagel, 1961; Widdowson, 1965). In Indian Arm the upper limits of *L. saccharina* vary from immediately below to 1 m below LLLW, the upper limits of *C. costata* vary from 0.5 to 1.5 m below LLLW, and the upper limits of *C. subulifera* vary from 1 to 3 m below LLLW.

Enteromorpha linza and *E. intestinalis* were observed by Rigg and Miller (1949) only in tide pools. In Indian Arm these plants were found in the intertidal region in areas lacking tide pools.

The vertical distributions of *A. cribosum*, *F. evanescens*, and *S. muticum* are essentially the same as described by earlier workers (Rigg and Miller, 1949; Neushul, 1965; Widdowson, 1965.

In Indian Arm the surface temperature is higher and the surface salinity lower than in those coastal areas in the northeast Pacific studied by earlier workers. The mean surface temperature and salinity in Indian Arm are 11.0 C and 14.2‰, whereas mean surface temperatures and salinities at sites

studied by earlier workers are 8.1–9.8 C and 30.3–31.3‰ (Fish. Res. Bd. Canada, Pacific Oceanog. Group, 1948, 1957; U.S. Coast and Geodetic Survey, 1962).

Wave action, which is considerable in areas studied by earlier workers, may account for some variation in the positioning of upper limits by minimizing desiccation of the algae during emergence or by physically removing delicate forms from the intertidal and upper subtidal regions. Alteration of vertical distributions by reducing or increasing desiccation would account for variation in the intertidal region only. Removal of delicate forms by physical action of waves would lower the upper limits of distribution in exposed areas. However, the upper limits of the sheltered Indian Arm species are either essentially the same or lower than those observed in more exposed regions.

Although submarine illumination and biotic competition are possibly important, the information available on these factors is inadequate for comparison between Indian Arm and those areas studied by earlier workers.

The available data suggest that the vertical distributions of algae in Indian Arm as compared with those of the same algae outside the inlet reflect their intolerance to the low salinity and high temperature of the surface water of the inlet.

Temperature and salinity have been suggested by numerous authors as possible factors determining the horizontal distributions of benthic organisms. Studies indicating the importance of these factors in the northeast Pacific have been made by Setchell (1935), Scagel (1961, 1963), Neushul (1965), and Widdowson (1965). If temperature and salinity are responsible for determining horizontal distributions, then it is axiomatic that in regions with stratification of these factors the same organisms will be oriented at depths determined by their tolerance to these factors.

Numerous examples are found in the marine animals of vertical displacement with latitude. The displacement, which has been attributed to the animal's response to unfavorable temperature regimes, was termed submergence by Ekman (1953).

Submergence of benthic algae was first reported along the southwest coast of North America by Gislèn (1944). Similar observations have been made in various European waters by Knight (1947), Levring (1957), Sundene (1953), and others. For the most part, these authors attributed in a general way the observed distributions to meteorological and oceanographic conditions. However, because of the presence of numerous undefined variables encountered in these earlier studies it was not possible to define the role of any one or a few factors with any degree of certainty. One notable exception is a study of a Norwegian fjord system by Jorde and Klavestad (1963) in which the horizontal and vertical distributions of benthic algae were related to water temperature, salinity, water movement, and submarine illumination. These authors observed a deepening of the upper limits of several algae from the fjord mouth to head, which they attributed to a general decrease in salinity over the same range.

CONCLUSION

From the evidence presented in this paper and elsewhere, temperature and salinity appear to be important factors in determining the distributions of marine benthic algae. In the estuarine environment, these factors may cause unfavorable conditions in the upper benthos. When the influence of these factors extends below the light compensation depth of the species, then the species will cease to exist in that area. For species restricted to the intertidal region, the depth of unfavorable temperature and salinity conditions for inhibiting the species will be much shallower.

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Scale Formation as Related to Growth and Development of Young Carp, *Cyprinus carpio* L.[1]

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ABSTRACT

Scales began to form on the body of young carp at 16–18 mm in total length. Scales first appeared anteriorly. The first row formed immediately below the lateral line, except for the posterior four or five scales being typically on the line. Later rows formed in succession above and below the first, each beginning anteriorly. Young carp acquired the typical structure and form of the adult fish by 21 mm. Squamation was completed on fish of 22–26 mm. The development of mouth parts, swim bladder, fins, and body scales appeared to be a function of length.

INTRODUCTION

The time and order of appearance of scales on the body of fish have been documented for only a few species. Elson (1939), in his study on the scales of the speckled trout, *Salvelinus fontinalis*, reviewed the literature on the teleost scale up to that time. More recent work is summarized by Van Oosten (1957) in a general discussion of the skin and scales of fish.

This paper describes the formation of scales on the carp, *Cyprinus carpio*, and relates squamation to the growth and general development of newly hatched fish.

MATERIAL AND METHODS

All carp used in the study were progeny of a population resident in the Nairn Island marshes of Lake St. Lawrence during the spring of 1965.

Scale formation and the development of body parts were studied on 406 carp ranging in total length from 5.0 to 33.0 mm. These fish were hatched from artificially fertilized eggs incubated in isolated ponds within the marsh. Growth data taken from these fish were supplemented by material provided by 225 young fish of known age taken randomly from populations established by the planting of fertilized eggs in several isolated areas within the marsh, and by 50 naturally spawned fish taken from the open marsh.

Scale formation was studied after the removal and preparation of the skin from the left side of the fish. The skin was placed in a 10% hydrogen peroxide solution for 10–30 min and then stained by immersion in an alizarin red solution for 5–10 min. Examination was made under low magnification.

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Growth

Newly hatched larvae averaged 5.2 mm (range 5.0–5.5) in total length. Differences in individual growth among the carp, influenced by water temperature, stocking density, and availability of food, had become pronounced by the 12th week of life. The fish then ranged between 98 and 113 mm in length and between 14 and 21 g in weight.

Development

The more obvious features of young carp, including mouth parts, swim bladder, and fins, had completed development in fish of 21 mm (Table I). Newly hatched fish, because of the large yolk sac, settled immediately on the bottom but at less than 6 mm were able to attach themselves to the aquatic vegetation and other parts of the substratum. By a length of 8 mm the yolk sac had typically disappeared and the fish swam with well-coordinated movements although all fins were still absent, or incompletely developed. At this length, the mouth had become functional and the fish fed actively on plankton.

The posterior part of the swim bladder first appeared at 5.5 to 6.0 mm and was filled with air taken at the surface as soon as the fish became free swimming at about 7 mm. The anterior part of the swim bladder did not appear until length of 11–12 mm and was not usually completely filled with air in fish of less than 15 mm.

The fins, apparent on newly hatched fish only as a pair of rudimentary pectorals and a continuous median fin fold, had become fully formed at 21 mm. At this size the fish had assumed the typical morphometry of adult carp. The pectorals became fully developed at 12–13 mm, the caudal at 18 mm, and the dorsal, anal, and pelvic fins at 20–21 mm.

Scale Formation

Scale formation was initiated in all fish at lengths between 16 mm and 18 mm inclusive (Table II). Partial scale formation occured between 16 and 25 mm. Scale formation was not complete on any fish of less than 22 mm but was complete on all specimens greater than 25 mm in length.

Scales appeared first on the anterior part of the body, immediately behind the operculum (Fig. 1). The first row developed immediately below the lateral line except in the region of the caudal peduncle, where the last 4 or 5 scales were typically on the lateral line. Later rows formed in succession above and below the first, each beginning anteriorly.

DISCUSSION

A review of the literature reveals that the order of squamation in the carp is at general variance with that recorded for other fish species in terms of both the location of the first scales and in the subsequent development of the scale pattern.

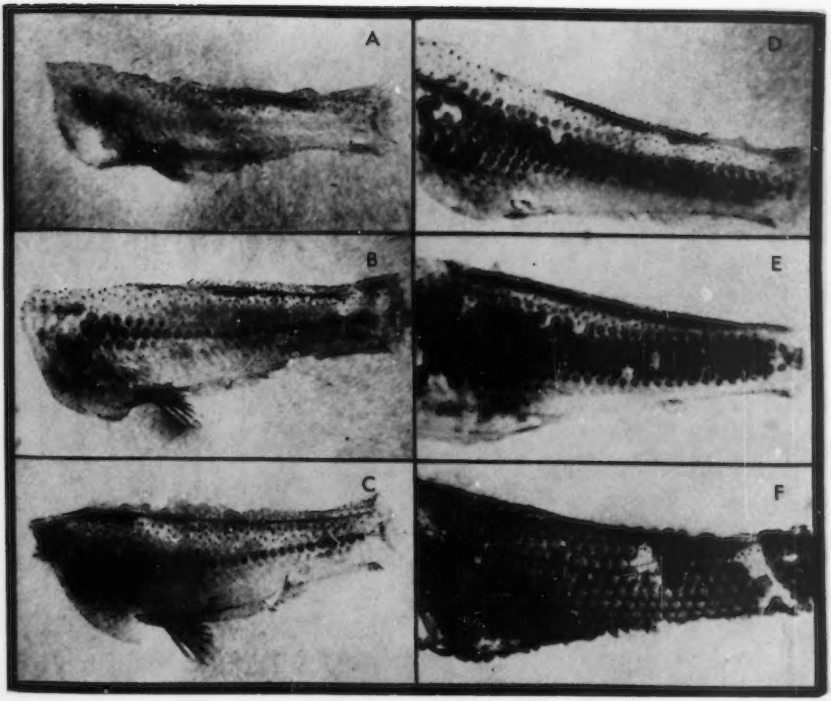

FIG. 1. The formation of scales on the body of young carp between 16 mm and 26 mm in total length. (Note: small dark spots dorsal to the lateral line are caused by pigmentation and are not scales.)

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TABLE I. Some aspects of the development of newly hatched carp with respect to total length.

Total length (*mm*)	Stage of development												
	Mouth	Free swimming	Yolk sac	Operculum	Filling of posterior gas bladder	Feeding	Fins					Filling of anterior air bladder	Body scales
							Pectoral	Dorsal	Caudal	Anal	Pelvic		
5	o[a]	o	x				o						
6	o	o	o	o			o						
7	x	o	o	o	o	o	o						
8	x	x		x	x	x	o	o	o				
9	x	x		x	x	x	o	o	o	o			
10	x	x		x	x	x	o	o	o	o			
11	x	x		x	x	x	o	o	o	o	o	o	
12	x	x		x	x	x	o	o	o	o	o	o	
13	x	x		x	x	x	x	o	o	o	o	o	
14	x	x		x	x	x	x	o	o	o	o	o	
15	x	x		x	x	x	x	o	o	o	o	o	
16	x	x		x	x	x	x	o	o	o	o	x	o
17	x	x		x	x	x	x	o	o	o	o	x	o
18	x	x		x	x	x	x	o	x	o	o	x	o
19	x	x		x	x	x	x	o	x	o	o	x	o
20	x	x		x	x	x	x	o	x	o	o	x	o
21	x	x		x	x	x	x	x	x	x	x	x	o
22	x	x		x	x	x	x	x	x	x	x	x	ox
23	x	x		x	x	x	x		x	x	x	x	ox
24	x	x		x	x	x	x	x	x	x	x	x	ox
25	x	x		x	x	x	x	x	x	x	x	x	ox
26–33	x	x		x	x	x	x	x	x	x	x	x	x

[a] o = partial; x = complete.

TABLE II. Development of the body scale pattern as related to total length in young carp.

Total length (*mm*)	Without scales	Partial row only	1–3 rows	4–5 rows	Well advanced	Completely scaled
11–15	162					
16	15	5				
17	5	5	1			
18	8	1	3	3		
19		4	3	5		
20		4	5	12	5	
21		1	5	6	2	
22				3	6	
23			2	2	8	4
24			1	1	10	40
25				1	2	21
26–30						45
Total	190	20	20	33	33	110

Among the salmonoids, scales have been reported to appear first more or less simultaneously along the lateral line (Elson, 1939; Cooper, 1951) with scale formation proceeding by the oblique extension of the scale rows from the primary lateral line papillae (Neave, 1936). Among the clupeids (Huntsman, 1919; Harrington, 1958), the escoids (Franklin and Smith, 1960), the centrarchids (Everhart, 1949; Ward and Leonard, 1954; Seifert, 1965), and the percoids (Priegel, 1964; Pycha and Smith, 1955) there seems to be general agreement that the first scales form in association with the lateral line and on the posterior part of the fish, frequently in the region of the caudal peduncle. However, Potter (1924) observed the first scales of the bluegill, *Lepomis pallidus*, to be scattered over the anterior part of the body.

Squammation and organogenis in the carp appeared to be closely related to the total length and proceeded according to a pattern peculiar to the species.

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Size at Maturity, Spawning Season, and Food of Atlantic Halibut[1]

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ABSTRACT

In otter-trawl catches of Atlantic halibut (*Hippoglossus hippoglossus* L.) by research vessels from 1959 to 1964, mature males less than 66 to 70 cm long were not regularly encountered. Males were 96 to 100 cm long before the majority were mature, and females slightly longer. The research catches and commercial samples taken by longline from 1961 to 1963 indicated that spawning occurred at various times during the first half of the year. Halibut up to 30 cm long ate invertebrates; from 30 to 80 cm, invertebrates and fish; and over 80 cm, fish almost exclusively.

INTRODUCTION

The Atlantic halibut continues to be the most highly prized groundfish landed on Canada's Atlantic coast. The Monthly Review of Canadian Fisheries Statistics for 1963 and 1964 indicates an average price of 31 cents and 32 cents per pound, respectively. However, landed price of halibut fluctuates widely, depending on demand, and fishermen often receive as much as 80 to 90 cents per pound for medium-sized fish. Total value of the landings from the Atlantic coast in the Maritimes, Quebec, and Newfoundland was about $1.6 million in 1963 and $1.4 million in 1964. Most of these landings were made in Nova Scotia, with Newfoundland usually receiving about 10 to 25% of the catch.

Because of difficulty in finding concentrations of halibut, the investigation of its biology and fishery has received less attention than such groundfish as cod and haddock. In 1946 and 1947, McCracken (1958) made a preliminary study of halibut in the northwest Atlantic area, particularly near the southeastern Canadian mainland. Later, he (McCracken, 1960) listed all known publications dealing with Atlantic halibut to 1960. The present author renewed studies on the Atlantic halibut in 1962. Information from tagging studies on distribution and movement has already been published (Kohler, 1964). Data on length at maturity, time of spawning, and food of the fish are presented here.

MATURITY STAGES AND SIZE AT MATURITY

Methods and Materials

Data were obtained from incidental catches of halibut taken in otter trawls on the research vessels *A. T. Cameron* and *Harengus* from 1959 to 1964. Maturity stages were studied by examining the gonads as they were taken from the fresh fish and classifying them according to the definitions in Table I.

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TABLE I. Definitions of maturity stages for halibut.

		Female	Male
Stage I	Immature	Ovaries small and firm, pale pink or reddish yellow. Membrane thin and somewhat transparent. Eggs invisible to naked eye.	Testes slender, resembling a clear, crimped, and slender string.
Stage II	Ripening 1	Ovaries slightly larger than in I but still small and firm. Contents microscopic. Eggs yellow or reddish yellow, opaque. Blood capillaries showing.	Testes increasing gradually in size; pinkish or flesh coloured. Blood capillaries showing.
Stage III	Ripening 2	Ovaries occupying about half of ventral cavity, reddish with numerous blood vessels. Minute opaque eggs visible to naked eye, giving the ovaries a granular appearance.	Testes occupying about half ventral cavity; beginning to turn white, with fine, rather conspicuous blood vessels. No milt running when pressure applied.
Stage IV	Ripe	Ovaries well developed, reddish golden, with blood vessels becoming inconspicuous. Some translucent eggs present among generally opaque mass of eggs. A few eggs extrusible by pressure on ovary.	Testes distinctly wavy, white and noticeably distended. Large lobes. A small amount of milt extrusible by pressure.
Stage V	Spawning	Ovaries very much developed. Eggs transparent or light amber colour and running freely.	Testes white and fully distended. Milt running freely at the slightest pressure.
Stage VI	Spent	Ovaries soft, flabby and bloody. Practically no eggs remaining; purple. Membrane starting to thicken and shrink, leaving surface whitish with purple showing through.	Testes shrunken and reddish. Vas deferens prominent against irregular surface of testes. Some blood left in organ.
Stage VII	Recovering	Ovaries beginning to take on pink or orange hue. Membrane still thick.	Testes resuming pale pink colour. Traces of blood in organ. Vasa deferentia wrinkled and string-like.
Stage VIII	Resting	Much like Stage I, but found in large fish. Ovary larger than in I. Membrane thicker and not as transparent as in I.	Testes larger than in I; surface regular; sometimes greyish pink.

As will be seen (Tables II–VIII), longliners fishing specifically for halibut catch larger fish on the average than are caught incidentally by otter trawlers. To ascertain the seasonal variation in gonad condition in these bigger fish, a special effort was made to gather data from them. Technicians put 5-gal cans containing 5 to 10% formalin solution aboard commercial longline vessels fishing for halibut. The crews were asked to save a sample of gonads from the fish caught during the trip. Since the fish were not measured, the condition of gonads cannot be related to particular size groups.

With one exception, the research catches for March to May (Table II) were taken in the International Commission for the Northwest Atlantic Fisheries (ICNAF) Division 4W (Fig. 1). One sample was taken further to the southwest, in ICNAF Division 4X. The rest of the research catches (Table III) were taken from July to October in Divisions 4V and 4W.

Results and Discussion

Most of the fish taken from March to May in the otter-trawl surveys were immature (Table II). Mature males were not regularly encountered until they were 66 to 70 cm long, and they were 96 to 100 cm long before the majority were mature. Females were slightly longer than 100 cm before the majority were mature.

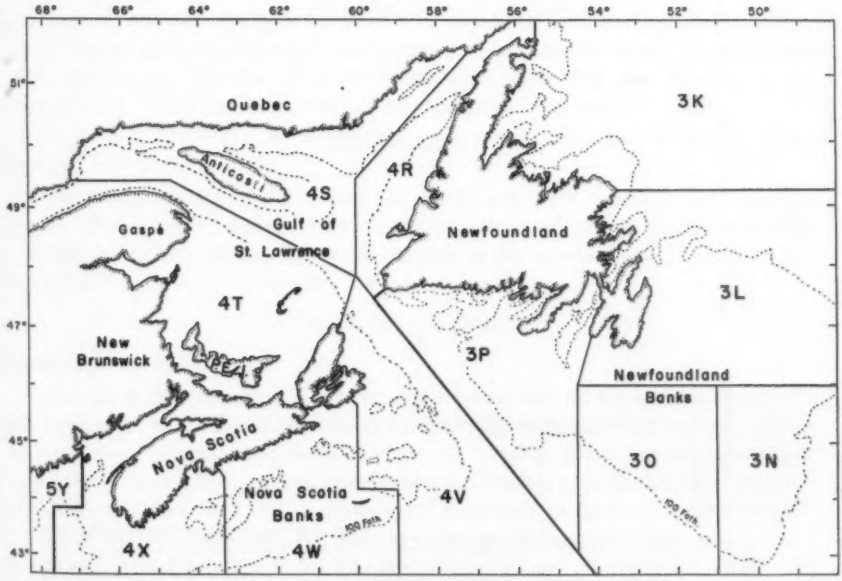

FIG.1. Divisions of the International Commission for the Northwest Atlantic Fisheries (ICNAF) area.

TABLE II. Numbers of male and female halibut of various lengths, taken by otter trawl during March to May 1959–1963 (cruises A6, A7, A20, A21, A37, A53, A66, A67 combined), in various maturity stages.

Length (*cm*)	Male				Female			
	Immature	Ripe-running	Spent-recovering	Total	Immature	Ripe-running	Spent-recovering	Total
11–15								
16–20	3			3	1			1
21–25					1			1
26–30	1			1	2			2
31–35	13			13	13			13
36–40	24			24	19			19
41–45	18			18	23	1		24
46–50	37		2	39	25			25
51–55	26			26	28			28
56–60	30			30	33			33
61–65	20			20	24	1		25
66–70	19	1	1	21	17		1	18
71–75	14	1	1	16	12			12
76–80	16	1	1	18	12			12
81–85	7	1	3	11	7			7
86–90	6	2	1	9	7			7
91–95	3	2		5	4			4
96–100			4	4	5		3	8
101–105			2	2	2			2
106–110	1	1		2			1	1
111–115		1		1				
116–120		1		1			2	2
121–125						2		2
126–130								
131–135						1		1
136–140						1	1	2
141–145								
146–150								
151–155								
156–160								
161–165								
166–170								
171–175								
176–180						1		1
181–185								
Totals	238	11	15	264	235	7	8	250

For mature fish of each sex about half were in pre-spawning to spawning stages, and half in spent-recovering stages. These data indicate that spawning in the 4W area is in progress during the March to May period.

In the otter-trawl surveys from July to October no spent or recovering halibut were taken (Table III), indicating that spawning was not occurring during this season. Again, the otter-trawl catches were mainly immature fish, mature males appearing at about 100 cm fork length.

Collections of longlined halibut from the Gulf of St. Lawrence fishery (Table IV) in May and June contained male and female gonads in both the ripening and spent-recovering stages. Later in the year, in the October, November, and L cember samples, most of the fish were ripening; four ripe female gonads were present in the December samples. The absence of spent-recovering fish in December, and their presence in the May samples, indicated that the main spawning in the Gulf of St. Lawrence probably took place from February to April.

Fewer samples of longlined halibut were collected from the Nova Scotia banks. The main data for this area were for February and March (Table IV). At that time there were both ripening and spent-recovering gonads in the collection. This would suggest, as did the research-vessel data, that spawning occurred in late winter and early spring.

More extensive longline data were available for the Newfoundland banks, particularly from March to June. In these months, the mature fish sampled were almost equally divided between the ripening and the spent-recovering stages. Those gonads classified as ripening were usually early in this stage during the spring months. This indicated that spawning also started in the winter on the Newfoundland banks and extended into the late spring.

These new data are in substantial agreement with the spawning times found by McCracken (1958).

Few halibut in the ripe or running condition were taken in any longline samples. Presumably, fish in this condition move off the fishing grounds or up in the water out of the range of longline gear, or else stop feeding during this period.

FOOD OF HALIBUT

Materials and Methods

As with maturity data, much recent information on food of halibut came from incidental otter-trawl catches of halibut during groundfish survey cruises. The data were summarized with a value of 1 being given for the occurrence of any particular type of animal in each halibut stomach. A preliminary examination of the data showed that a meaningful summary of stomach contents could be obtained if all data from Nova Scotia banks cruises were combined and if the fish were grouped into 10-cm length groups. Further examination showed no differences in food preferences between males and females so these data were also combined. The procedure on board the *A. T. Cameron* did not allow for

TABLE III. Numbers of male and female halibut of various lengths, taken by otter trawl during July to October 1960–1964 (cruises A30, H29, A88 combined), in various maturity stages. (No male or female halibut were taken in the spent-recovering stage.)

Length (*cm*)	Male			Female		
	Immature	Ripe-running	Total	Immature	Ripe-running	Total
11–15						
16–20						
21–25	1		1	1		1
26–30				4		4
31–35	8		8	10		10
36–40	8		8	2		2
41–45	5		5	2		2
46–50				1		1
51–55	3		3	4		4
56–60	3		3	2		2
61–65	3		3	3	1	4
66–70	6		6	4		4
71–75				2	1	3
76–80	2		2	1		1
81–85	2		2			
86–90				1		1
91–95	1	2	3	1		1
96–100						
101–105		1	1			
106–110		1	1	1		1
111–170[a]						
171–175					1	1
Totals	42	4	46	39	3	42

[a] No samples.

[a] No samples.

TABLE IV. Numbers of male and female halibut, taken by commercial longliners in various months from 1961 to 1963, whose gonads were in various maturity stages.

	Gulf of St. Lawrence				Nova Scotia banks				Newfoundland banks			
Month	Immature	Ripening	Ripe-running	Spent-recovering	Immature	Ripening	Ripe-running	Spent-recovering	Immature	Ripening	Ripe-running	Spent-recovering
Jan.												
Feb.					5♂; 12♀	7♀		1♂; 21♀				
Mar.					5♀	1♀			9♂; 32♀	4♀		5♂; 10♀
Apr.									8♂; 11♀	5♀		12♂; 8♀
May	1♂; 15♀	3♀		9♂; 4♀					1♂; 3♀	2♂; 21♀		3♂; 2♀
June	5♀	2♂; 3♀							11♀	6♀		1♂
July					5♀	2♀						
Aug.												
Sept.									4♀	1♂; 6♀		
Oct.		8♂; 2♀		2♂						2♂; 3♀		
Nov.	1♂; 2♀	11♂; 2♀			5♂							
Dec.	7♂	2♀	4♀									

identification to species of the majority of the food items found. For this reason the items were classified into seven major groups (Table V).

As with gonad collection, samples of stomachs were obtained from fish caught by commercial longline vessels. Stomachs and gonads were usually collected and preserved in formalin solution at the same time by the fishermen, so the samples referred to came from the same commercial trips as those shown in the maturity studies. In summarizing this material, after examination of individual samples, they were combined by months. However, as with the maturity data, the information was divided by areas: Gulf of St. Lawrence, Nova Scotia banks, and Grand Bank area.

To relate the food data to sizes of fish, a stomach weight/fish length relationship was worked out from survey cruise collections. To provide this relationship, stomachs were cut out of the digestive tracts at the same relative places at the posterior end of the oesophagus and at the pyloric valve. They were preserved in 5 to 10% formalin solution. The contents were examined after the cruise, and then the empty stomachs were weighed in grams and the weight was recorded with the fish length. An arithmetic plot of the 137 pairs of observations indicated a curvilinear relationship. The data were therefore plotted on double log paper (Fig. 2) together with a straight line fitted to the data. From this graph, a table relating stomach weight and fish length was constructed.

When the commercial longline stomach samples were examined, the food was removed and the type recorded. Then the stomachs were removed and weighed in the same way as those from the research-vessel catches. The fork length corresponding to the respective stomach weight was then read from the table.

Results and Discussion

The most interesting feature of the food data collected from the halibut in the research-vessel catches was the change in diet with increasing size (Table V). Fish up to about 30 cm contained invertebrate food almost exclusively, mostly annelids and crustaceans. Those from 30 to 80 cm in length contained either invertebrates or fish or both. Halibut over 80 cm in length fed almost exclusively on other fish. Here again, the data were limited by the smaller size of fish in the otter-trawl catches.

Although the commercial longline data for larger fish (Tables VI–VIII) are separated for the Gulf of St. Lawrence, Nova Scotia banks, and Grand Bank area, the results were generally similar. In stomachs that contained food, fish remains were by far the most prevalent item, but the remains, consisting often of fish bones, were not identified to species. There were a few records of large invertebrates.

One would expect that halibut would tend to select large items of food as they grew to a larger size. Halibut are known to have a relatively fast rate of growth for flatfish, particularly in the ages over 10 years (McCracken, 1958, Figs. 11–15). To support this rapid growth and large ultimate size, quantities

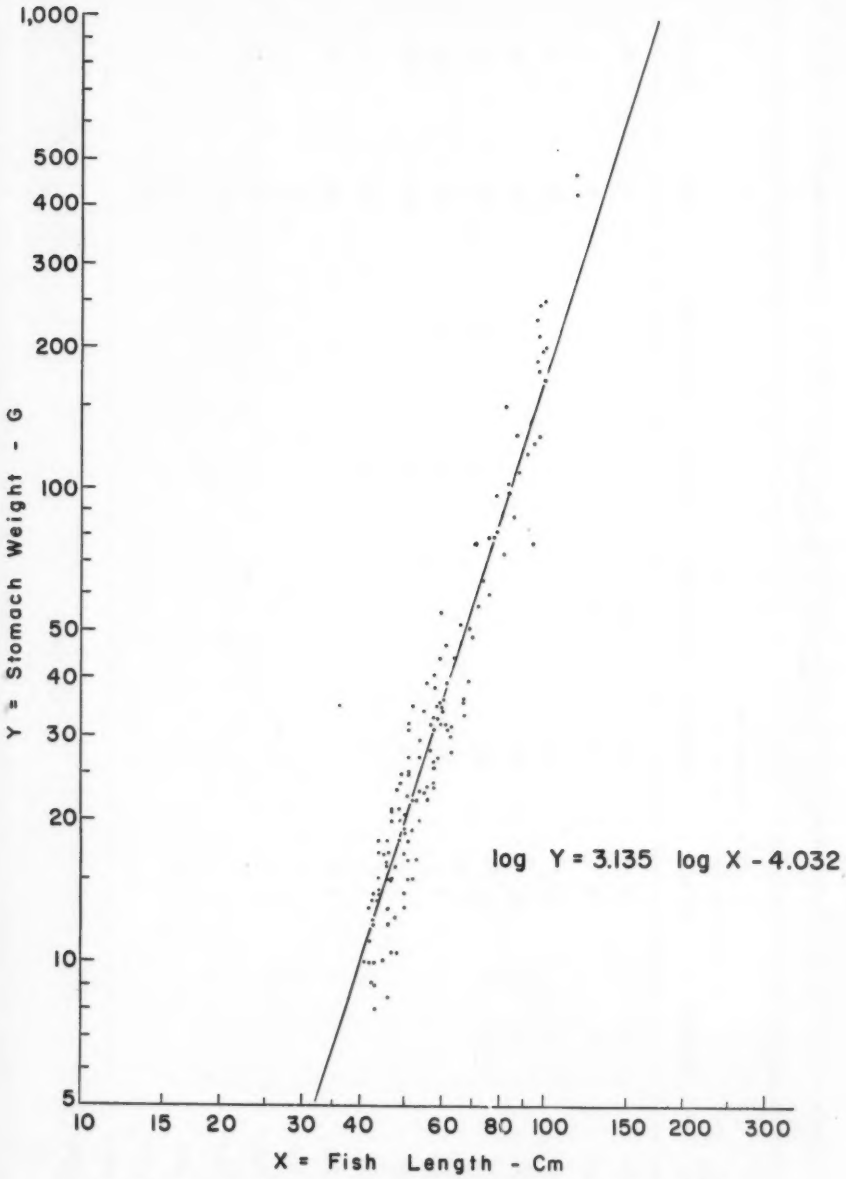

FIG. 2. The relation between stomach weight and fish length in halibut.

TABLE V. Numbers of occurrences of various food items in otter-trawled halibut, Nova Scotia banks (*A. T. Cameron* cruises 6, 7, 18, 20, 21, 37, 53, 66, 67, 88 combined; 655 halibut).

Length (*cm*)	Annelids	Crustaceans			Molluscs	Echinoderms	Fish	Empty
		Crabs	Shrimps	Unidentified				
11–20	2	5	14	4			1	6
21–30	1	4	4	2			1	2
31–40	2	9	25	3	1		22	20
41–50	1	13	56				35	26
51–60	1	12	46	2	3	2	53	41
61–70		5	21		2	2	55	37
71–80			3		1		43	21
81–90			1		1		30	11
91–100		1					20	11
101–110							12	3
111–120							4	1
121–130							4	
131–140							3	
141–150							1	
151–160								
161–170								
171–180					1		1	

TABLE VI. Numbers of occurrences of various food items in halibut taken by commercial longliners, Gulf of St. Lawrence (157 fish).

Length (*cm*)	Empty	Bait	Unidentified	Lumpfish	Skate egg case	Redfish	Haddock	Cod	Fish eggs	Sea urchin	Crab
1–70 [a]											
71–80	3		1								
81–90	5	1							1		
91–100	8		3								
101–110	11	3	5								
111–120	7	1	6				1	1			2
121–130	12	1	5					1			
131–140	9	1	3								1
141–150	10		8	1						1	
151–160	7	1	6			1					
161–170	5		8		1	1					
171–180	4	1	1								1
181–190	2	1									
191–200	1		1								
201–210											
211–220	1		2								
221–230			1			1					
231–240											
241–250			1								
251–260	1										

[a] No samples.

TABLE VII. Numbers of occurrences of various food items in halibut taken by commercial longliners, Nova Scotia banks (152 fish).

Length (*cm*)	Empty	Bait	Unidentified fish remains	Crab	Flatfish	Brittle stars	Redfish	Pelecopod	Hagfish	Fish eggs	Bank clam
1–50 [a]											
51–60	1										
61–70	4		2	2							
71–80	6		5	1							
81–90	15	1	3		2						
91–100	16		6								
101–110	6		7								
111–120	11		7							1	
121–130	4	2	7	1							
131–140	1		3				2				
141–150	3	1	6								
151–160	3	1	3	1							
161–170	3		3								
171–180			2	1					1		1
181–190	2	1	1					1			
191–200			3		1	1					
201–210											
211–220											
221–230	1										
231–240			1								

[a] No samples.

[a] No samples.

TABLE VIII. Numbers of occurrences of various food items in halibut taken by commercial longliners, Grand Bank area (185 fish).

Length (*cm*)	Empty	Bait	Unidentified fish remains	Redfish	Crab	Flatfish	Cod	Haddock	Eelpout	Sculpin	Whelk
1–70 [a]											
71–80	2										
81–90	6		1								
91–100	8		5								
101–110	12		9	1	1						
111–120	13		8		1	1					
121–130	11		4		1					1	
131–140	14	1	5			1					
141–150	9	2	7		2			1			
151–160	5		8			1				1	
161–170	6		8			1					
171–180	2		5						1		
181–190			3			2					
191–200	1		1			1					
201–210	1		5					1			
211–220	1	1	3		1		1				1
221–230											
231–240			2								
241–250			1								

[a] No samples.

of food that are relatively easily available would have to be selected. This would tend to restrict halibut to a fish diet in the areas sampled.

ACKNOWLEDGMENTS

I thank the staff of groundfish investigations at St. Andrews and Fisheries Research Board technicians at various fishing ports who helped to collect the data used here. Particular recognition is given to R. K. Robicheau who helped in the analysis. The assistance of commercial fishermen in collecting gonad and stomach samples was much appreciated.

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Effects of Feeding on the Thyroid, Kidney, and Pancreas in Sexually Ripening Adult Sockeye Salmon (*Oncorhyncus nerka*) [1,2]

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ABSTRACT

In unfed adult sockeye salmon, *Oncorhynchus nerka*, histological examination showed extensive degenerative changes in the thyroid, pancreas, and kidney during gonad development. The more pronounced changes were generally noted in starved fish spawned in the wild. Feeding either prevented (thyroid) or distinctly reduced (pancreas, kidney) these changes in the sexually ripe fish. In fed spent sockeye the thyroid showed little change, the kidney exhibited further deterioration although not as marked as in the corresponding unfed fish, but the pancreas showed marked degenerative changes comparable with those exhibited in the unfed.

INTRODUCTION

A considerable body of information is now available regarding the histological and chemical changes that occur in the adult Pacific salmon (genus *Oncorhynchus*) during sexual maturation (Greene, 1913; Idler and Tsuyuki, 1958; Oguri, 1960; Robertson and Wexler 1960). Why these fish die after their first spawn, however, continues to be a matter for speculation. Robertson et al. (1961, 1963), in studies using trout (*Salmo gairdneri*) and adult Pacific salmon, examined the relation between elevated 17-hydroxycorticosteroid blood concentrations, the degenerative changes that occur in the sexually ripening salmon, and the death of the animal after spawning. He concluded that the principal histological changes and the death of the spent salmon were, in all probability, the result of an abnormally high concentration of blood 17-hydroxycorticosteroids. It is a matter of record, however, that whereas there is a substantial amount of evidence to indicate a marked elevation in the plasma 17-hydroxycorticosteroid concentrations in sexually ripening migrating adult salmon, there are exceptions (Schmidt and Idler, 1962; U. H. M. Fagerlund, unpublished data). One plausible explanation for this may be found in the fact that investigations into the death of the salmon have been confined, primarily, to fish obtained from their natural habitat.

Field studies have clearly shown that elevated water temperatures, pollution, disease, and forced delays in completion of the migration can result in significant prespawn mortalities (Wood, 1965). Furthermore, studies indicate that the method of capturing fish, and also the conditions of captivity, can

[1]Received for publication June 9, 1966.
[2]The second paper in a series on the post-spawning death of sockeye salmon.

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induce pronounced physiological changes in a short period of time. Salmon captured in the sea and held in a tank aboard ship exhibited a marked increase in plasma 17-hydroxycorticosteroid concentration within the first 2 hr of captivity; at the end of 48 hr the plasma corticoid concentration of these fish had risen fourfold (Hane et al., 1966). Leloup-Hatey (1958) in studies with carp (*Cyprinus carpio L.*) reported a marked increase in the plasma corticoid concentration of those fish which had been frightened before capture. In an attempt to eliminate or at least control these stresses and thus achieve a clearer understanding of the changes which occur during gonad development, a study was initiated in which adult sockeye were held in captivity during the period of sexual development and spawning. Additionally, the finding that these fish would feed in fresh water afforded the opportunity to study the effect(s) of starvation. The preliminary results of this continuing study have been reported (McBride et al., 1965). The purpose of the present phase of the study was to investigate, using histological methods, the extent of changes that occur during gonad development in the thyroid, kidney, and pancreas of both fed and unfed adult sockeye. Reports on various other andocrine organs will follow.

MATERIALS AND METHODS

Fish

As in the work reported earlier, adult migrant sockeye were captured at the entrance to Great Central Lake, Vancouver Island, B.C., during June and July while still in a "sea-green" condition. The method of capture, their transportation to the laboratory, prophylactic and disease treatments, as well as general cultural methods have been described (McBride et al., 1963). Some 2 weeks after capture the salmon were divided into two groups, and feeding of one group began (see below). The second group was held as the unfed control. When the fish were judged to be sexually ripe they were spawned as outlined in the preceding report (McBride et al., 1963).

Food

In the initial study referred to above, the fish were fed marine zooplankton (predominantly *Euphausia pacifica*). This diet, although readily accepted by the fish, was found to be nutritionally deficient. In the present investigation two diets were used: Halver's synthetic mixture (Woodall and LaRoche, 1964), a diet designed specifically to meet the nutritional requirements of trout and juvenile salmon; and a mixture of beef liver, beef heart, mixed cereal (Pablum),[3] and canned salmon, a diet which had been used successfully in an earlier study with adult salmon (McBride et al., 1963). Although the latter diet has been the standard fish food in use at this laboratory for both trout and salmon for a number of years, a high incidence of kidney disease has occurred in salmon after 9 to 10 months of daily feeding. However, it is not certain if there is any

[3]Registered trade name, Mead Johnson of Canada Ltd.

relation between the disease and the daily feeding of the diet for prolonged periods.

Before the fish could be induced to accept either of the diets, a period of conditioning was necessary. This entailed first offering the fish only zooplankton, which they readily accepted; after a few days the test diet was added to the zooplankton, the initial ratio being 80% zooplankton to 20% test diet. After a few additional days feeding of this mixture, the zooplankton content was gradually reduced until the fish were eating only the test diet.

Due to space limitations it was not feasible to carry out this study in a single year. Thus during 1964–1965 the fed fish were supplied after a suitable conditioning period with Halver's diet whereas in the second year, 1965–1966, the fish were given the natural food. Feeding was carried out once each day, the food being partially thawed and cut into 1-cm cubes. Food was supplied until all the fish appeared to be satiated.

Histological Techniques

Methods of tissue sampling, fixation, embedding, and sectioning were those used previously (McBride et al., 1965). All sections were cut between 4 and 5 μ thick. Kidney tissue was taken from the midportion of the organ. Sections were stained with Mayer's hematoxylin and eosin for general structural examination. Special stains employed were: Masson trichrome for collagenous tissue; periodic acid Shiff for colloid of the thyroid gland; and Gomori aldehyde fuchsin alone or in combination with Masson trichrome as a counterstain, for differentiation between the α and β cells in the islets of Langerhans (Pearse, 1961).

Tissue samples were collected from 16 sexually immature, sea-green adult sockeye, 25 sexually ripening fish (17 fed, 8 unfed), and 34 fish spawned in captivity (17 fed, 17 unfed). In order that a comparison might be made between fish spawned in captivity and in their natural habitat, samples of the tissues were also obtained from eight spent or spawning fish at the mouth of Lindsay Creek, Great Central Lake.

RESULTS

Behaviour

During the first 2 weeks of captivity the fish showed little interest in feeding. At this time they were highly excitable, reacting swiftly and often violently to sudden distractions. By the 4th week the majority of the fish had settled into a characteristic behaviour pattern which prevailed until they were close to sexual ripeness. They formed tight, compact schools and except during feeding individual fish were rarely seen leaving the group for periods longer than a few seconds. During feeding the majority remained in the shaded area of the tank, avoiding any close contact with the feeder. A few of the more agressive salmon would, however, dart into the open for food, but returned just as quickly to the school. Conditioning of the fish was completed in 3 weeks with Halver's diet and in 2 weeks with the natural food. In a few trial tests carried out with

approximately 20 fish on three or four occasions during each year, most of the fish showed an apparent preference for the meat diet. During both years a considerable variation in food consumption was evident. A few fish, approximately 10%, were consistently heavy feeders eating between 1.0 and 2.0% of their body weight daily, whereas about an equal number of fish ate only sparingly or not at all. The majority of the fish consumed between 0.5% and 1% of their body weight in food each day.

Some 2–3 weeks before reaching sexual ripeness a distinct change was noted in the behaviour of both fed and unfed sockeye. At first, the deviations in behaviour were subtle with only a few fish involved. This may be due, in part, to the fact that the fish do not all mature at the same rate. The fisrt variation noted was the random wandering of the female, often followed by several males, from the school for periods of up to several minutes. It was common for a female to repeat this move several times within a relatively short period. Where the school had been compact, it was now gradually spreading out and the fish for the first time began moving into and staying in the lighted areas of the tank. Occasionally, fights were seen between males or between females and, whereas a female would chase or ward off a male, the male was never seen attacking the female. This aggressiveness appeared to reach its climax during spawning. On more than one occasion a female that was not quite ready to spawn attacked and destroyed her mate. In the female, aggressiveness did not abate until several weeks following the completion of spawning. In the male it persisted for 2 or 3 weeks beyond the completion of spawning of the last female in his sphere of influence.

Feeding at this time was sporadic; a few fish remained consistently heavy feeders up to and after spawning but the majority showed a distinct decrease in their food consumption. It was common to have a fish feed actively 1 day, then avoid food for 2 or 3 days, only to commence feeding again.

Utilization of Diets

The total solids of the muscle of fish fed Halver's mixture differed little, if any, from that of those fed the natural diet. Indeed, the dry weights of the muscle expressed as percentages of total wet weights from spent fish fed Halver's diet (17.9%) and the natural diet (17.8%) were comparable to that found in the preceding study where the fish were fed zooplankton exclusively (17.6%) and only slightly higher than that of the muscle of unfed fish (16.3%). Thus, although the samples were few and the sampling did not cover all phases of sexual development, it appears that feeding had little effect in delaying or preventing the degeneration of the skeletal muscle. This aspect of the work has been described in greater detail elsewhere (Tomlinson et al., 1967).

Histological Changes

The histological changes that occurred in the thyroid, pancreas, and kidney of both fed and unfed adult sockeye during sexual development are summarized in Table I. The influence of feeding was the same regardless of the diet used.

TABLE I. Histological changes in the thyroid, pancreas, and kidney during gonad development of fed and unfed adult sockeye from Great Central Lake.

Organ	Condition of fish			
	Fed ripe	Unfed ripe	Fed spent	Unfed spent
Thyroid	Follicles small and numerous; colloid dense.	Follicular epithelium involuted and atrophied.	No apparent change.	Degeneration.
Kidney	A few glomeruli showing capillary sclerosis.	Many glomeruli showing capillary sclerosis.	Increase in glomerulo-capillary sclerosis.	Marked degeneration of glomeruli.
Pancreas				
(i) Exocrine	Cells well granulated and normal in appearance.	Extensive loss of cytoplasm; many pycnotic nuclei.	Marked degeneration.	Marked degeneration.
(ii) Endocrine	Some apparent increase in islet number.	Hypertrophy as well as increase in number of islets.	Hypertrophy and hyperplasia of islets.	Hypertrophy and hyperplasia of islets.

Thus, no distinction is made in the histological results between the two groups of fed fish.

THYROID

The thyroid follicles of the sea-green or sexually immature adult fish were numerous, generally small (<100) and filled with a dense homogeneous colloid (Figs. 1, 2). Resorption vacuoles were few and in most instances present in only a small number of the follicles examined in any one fish. The follicle epithelium was uniform in height, the average cell height of 10 follicles measured in each of nine fish was 4.9μ.

In the unfed, sexually ripening fish a progressive decrease in thyroid activity was indicated by the size, apparent number, and appearance of not only the follicles but also the thyroid cells. Although the number of fish examined was not sufficient to enable a definite conclusion, the evidence obtained suggests that the increase in the proportion of large follicles (>150 μ) paralleled the rate of maturation of the gonad. By the time of spawning the number of large follicles exceeded in most instances the number of small follicles (<100 μ). The colloid was very dense, but occasionally many follicles, both large and small, contained a few resorption vacuoles (Figs. 3, 4). Cellular atrophy was particularly pronounced in the very large follicles (>200 μ), where there was a decrease

in both cell number and height, the latter rarely exceeding 1.5 μ. The average cell height of 10 follicles measured in each of seven fish spawned in captivity was 2.4 μ. Although the thyroid of those fish which had spawned in their natural habitat closely resembled that of the comparable unfed fish in captivity, the cell height of the former was lower (< 2 μ).

Feeding, especially where it was active appeared to have prevented changes in the thyroid even in the spent fish (Figs. 5, 6). In the spent fed fish, few large follicles were evident; the colloid varied in intensity from dense to light and contained numerous peripheral vacuoles. The height of the follicular epithelium was equal to and in some fish exceeded that noted in the sea-green fish. Indeed, the cells of a few follicles were high columnar (10–13 μ). The average cell height of 10 follicles measured from each of six of these fish was 4.7 μ. Also, there was an apparent increase in follicular cell number. Where feeding had been light or sporadic the thyroid exhibited an increase in the proportion of large follicles with a varied reduction in follicular epithelium.

Kidney

The structural changes which occurred in the kidney during gonad development were delayed and reduced but not prevented by feeding. Sclerosis of the glomerular capillary bed, the most common degenerative change, was evident in only a few of the sea-green fish (Fig. 7). The change in these fish was limited to a slight thickening of the capillary channels. In the unfed spent fish this degenerative process had progressed to a point where many of the glomerular tufts appeared as masses of connective tissue. The kidneys of the fed spent or fed sexually ripe but unspawned fish exhibited intermediary stages between these two extremes. It was not uncommon to find glomeruli from fed spent fish which resembled those of the sea-green fish (Fig. 9). Kidneys from these fish did, however, contain other glomeruli in a moderate or, occasionally, in an advanced state of sclerosis.

Thickening of Bowman's capsule, although not noted in the sea-green fish, was present in many of the sexually ripe or spent fish, both fed and unfed. Again, this degenerative process appeared to be more prevalent and advanced in the unfed spent than in the fed spent fish.

A decrease in the number of lymphoid cells and a concomitant increase in the pigmentation of the kidney parenchyma which occurred during gonad ripening did not appear to be altered by feeding.

Alterations in the kidney tubules were confined with one or two exceptions to the spent fish. Tubule changes were limited to a loss of some cytoplasm and usually only a few tubules were involved. Although no instances were noted where this degenerative change was widespread, its occurrence was nevertheless more frequent and pronounced in the unfed fish.

The degenerative changes in the kidney of unfed fish spawned in their natural habitat were generally more pronounced than noted in comparable unfed fish held in captivity (Fig. 8).

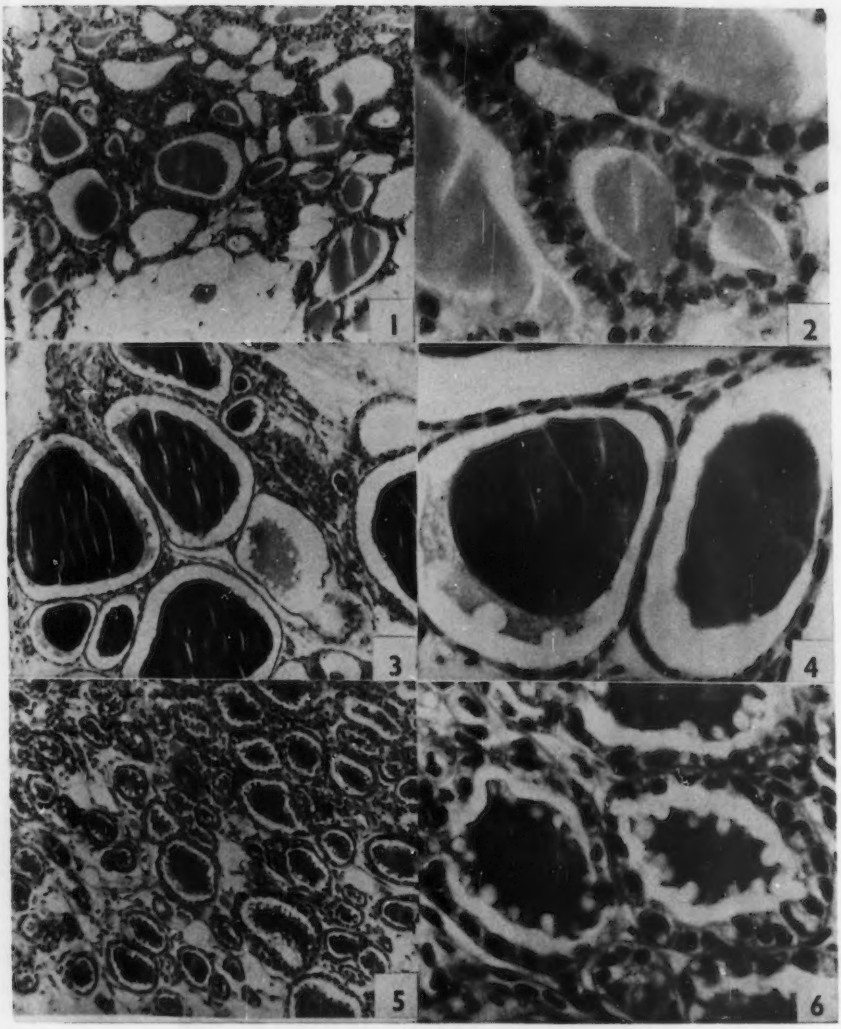

FIG. 1. Thyroid tissue of adult sea-green sexually immature sockeye. The follicles are numerous and small. Resorption vacuoles are rare and when present are generally confined to the smaller follicles. Hematoxylin and eosin; ×90.

FIG. 2. Higher magnification of thyroid tissue shown in Fig. 1. Follicular cells cuboidal, about 6 μ in height. The colloid appears to be homogeneous and dense. Periodic acid Shiff and hematoxylin; ×350.

FIG. 3. Thyroid of unfed sockeye spawned in captivity. Follicles are greatly enlarged and include a flattened epithelium which appears to contain a generally dense colloid. Resorption vacuoles are evident in many of the follicles, but are few in number. Hematoxylin and eosin; × 90.

FIG. 4. Enlargment of the two smaller follicles at the left-hand corner of Fig. 3. Follicular cells about 2 μ in height. Hematoxylin and eosin; ×350.

FIG. 5. Thyroid of fed sockeye spawned in captivity. Follicles numerous, small, and filled with a dense colloid. Hematoxylin and eosin; ×90.

FIG. 6. Higher magnification of thyroid tissue shown in Fig. 5. Follicular cells cuboidal, about 5 μ in height. The homogeneous and dense-appearing colloid shows many resorption vacuoles. Hematoxylin and eosin; ×350.

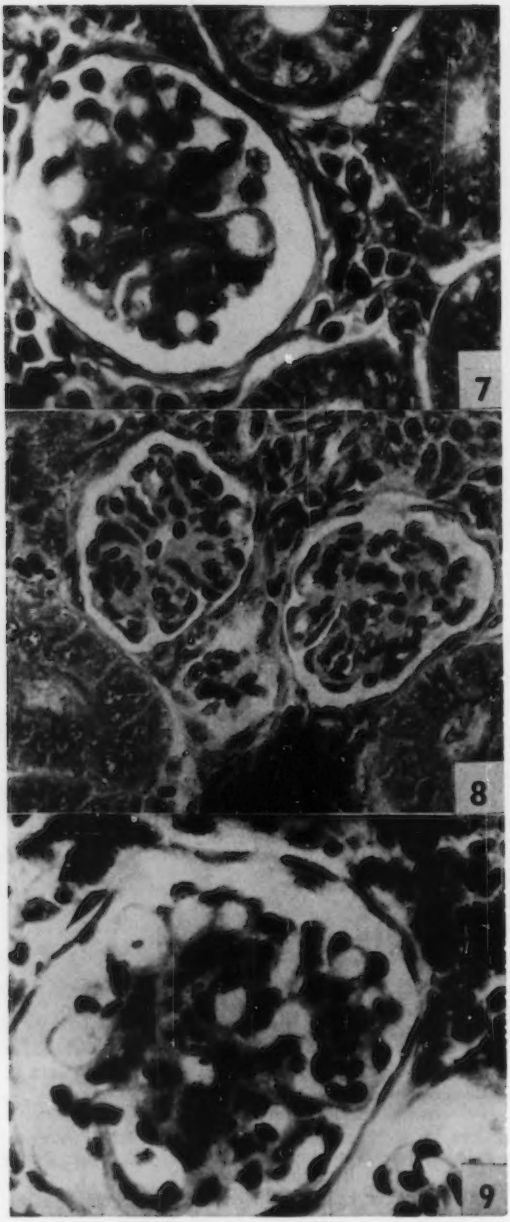

FIG. 7. Kidney of adult sea-green sexually immature sockeye. Glomerulus normal in appearance except for slight thickening of the capillary channels. Hematoxylin and eosin; ×430.

FIG. 8. Kidney of unfed sockeye spawned in its natural habitat, showing marked capillary glomerulosclerosis. Hematoxylin and eosin; ×430.

FIG. 9. Kidney of fed sockeye spawned in captivity. Glomerulus normal in appearance. Hematoxylin and eosin; ×430.

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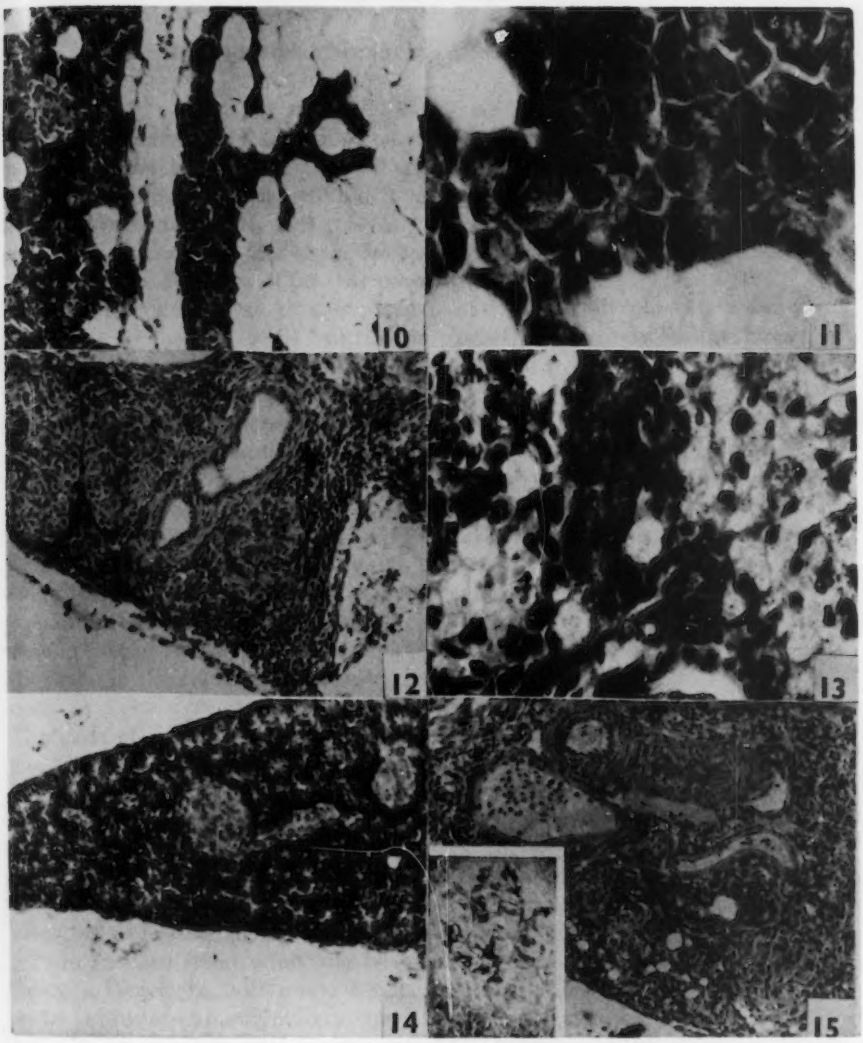

FIG. 10. Pancreas tissue of an adult sea-green sexually immature sockeye. Pancreas tissue embedded in the fat of the omentum. A small islet of Langerhans is visible at the top left half of the photo. Hematoxylin and eosin; ×90.

FIG. 11. Higher magnification of the exocrine portion of the pancreas shown in Fig. 10. Zymogen granules are abundant in acinar cells. Hematoxylin and eosin; ×350.

FIG. 12. Pancreas of unfed sexually ripe but unspawned sockeye. Note proliferation and increase in size of the islets and absence of the fatty layers of the omentum. Gomori's aldehyde fuchsin; ×90.

FIG. 13. Section of same pancreas as shown in Fig. 12, but at a higher magnification. Exocrine tissue in various stages of degeneration. Zymogenous cells generally degranulated and many of the nuclei pycnotic. Gomori's aldehyde fuchsin; ×350.

FIG. 14. Pancreas of fed sexually ripe unspawned sockeye. Zymogenous cells well granulated. Of the two islets present, one appears to have been increasing in size. Gomori's aldehyde fuchsin; ×90.

FIG. 15. Pancreas of fed spent sockeye. Compare this section with that shown in Fig. 14. Note marked increase in number of islets. Exocrine tissue in various stages of dissolution. Hematoxylin and eosin; ×90. Inset (Gomori's aldehyde fuchsin; ×90) shows an islet from the same fish which contains a few deep staining (heavily granulated) β cells.

PANCREAS

The pancreas of Pacific salmon consists of two portions, exocrine and endocrine, and is a diffuse tissue dispersed between and around the pyloric caeca. The endocrine part, referred to as the islets of Langerhans, is embedded in the exocrine tissue. If, as is generally the case with the adult sea-green sockeye, the fish has been feeding actively, the caeca as well as the pancreas are often engulfed in layers of fat, the omentum (Fig. 10).

Sexual ripening was characterized in the unfed, but not in the fed fish, by structural changes in the exocrine portion of the pancreas. In the former, a decrease in the amount of this tissue was indicated by a visual shrinkage in the size of the caeca as well as by a reduction in the amount of exocrine, or zymogenous, tissue seen microscopically (Fig. 12). The diffuseness of the pancreas rendered accurate quantitative measurements as to the amount present impossible. The exocrine cells of the unfed ripe fish were atrophied and in a few fish focal areas of degeneration were evident (Fig. 13). In the fed ripe sockeye the pyloric caeca were approximately equal in size to those of the sea-green fish, and little, if any, change was apparent in the amount of exocrine tissue (Fig. 14). The granulation of the zymogenous cells appeared similar to that seen in the sea-green fish (Fig. 11). The spent fish, both fed and unfed, exhibited a reduction in the size of the caeca and in the amount of exocrine tissue from that seen in the corresponding ripe but unspawned fish (Fig. 15). The degenerative changes were, however, more pronounced in the unfed spent salmon. The cells of what little exocrine tissue remained were largely degranulated and the nuclei were in various stages of dissolution. In the starved sockeye, the disintegration of much of the basement membrane gave the exocrine tissue a disorganized appearance. The average length of six caeca from each of four fish in the different groups were as follows: sea-green, 22.2 mm; unfed spent, 6.1 mm; and fed spent, 17.2 mm. It is conceivable that the shrinkage in the length of the caeca of the fed spent fish was a direct reflection of the reduction or cessation of feeding that occurred just before and during spawning.

In the sea-green adult the islets of Langerhans were small and few in number. Generally, both α and β cells were well granulated and they appeared to be present in approximately equal numbers.

Sexual development was accompanied in both fed and unfed fish by hyperplasia of the endocrine tissue. Also, in the unfed but not in the fed fish an increase occurred in the islet size. The islets, which seldom exceeded 100 μ in the sea-green adult, were appreciably larger in the maturing unfed fish, the majority exceeding 150 μ (Fig. 12). The increase in the number of islets in the fed fish did not appear to equal that in the corresponding unfed fish. With the possible exception of the small islets, where generally both groups of cells appeared to be well granulated, no consistent pattern in the granulation of either cell type was noted. Among the large islets it was common to find the cells well granulated in one and almost completely degranulated in another from the same fish.

As it had in the exocrine tissue, spawning appeared to accentuate structural changes in the endocrine tissue of both groups of fish. Again, however, the most

pronounced degeneration was seen in the unfed fish. Where the majority of the islets of the starved spent sockeye exceeded 250 μ, those of the corresponding fed fish were rarely above 200 μ. The α and β cells of the unfed salmon, like those of the fed fish, varied from well granulated to what appeared to be almost complete granular exhaustion. In a few of the larger islets of the unfed fish the cytoplasm appeared to be "moth eaten" and many of the nuclei appeared to be disintegrating.

During the period of sexual development the ratio of α to β cells in the small islets appeared to remain constant. In the large islets the faint tinctorial characteristics of many cells made any distinct differentiation difficult, but it appeared that there were more α cells than β cells.

The fat of the omentum, conspicuous in the caecal area of the adult sea-green fish, was rapidly depleted in the unfed salmon. Indeed, in most cases visual examination indicated a complete exhaustion of this fat depot by the end of the 6th week of captivity. Feeding, with the exception of a few early and active feeders, had little apparent effect in delaying this depletion. Of those which fed actively a few exhibited a visibly reduced amount of fat in the omentum at the time of sexual ripeness but in all the spent fish this fat depot had disappeared.

The pancreas of those fish which spawned in their natural habitat exhibited all the degenerative changes seen in the corresponding unfed fish spawned in captivity.

DISCUSSION

The results of the present investigation indicate that feeding prevented the deterioration of the thyroid and delayed and reduced the deterioration of the kidney and pancreas in adult sexually ripening sockeye. The beneficial effects of feeding were not, however, as clearly discernible in the fish after spawning. In such fish, the pancreas of the fed, like that of the unfed, exhibited signs of marked disintegration. The degenerative changes in the kidney of the fed spent fish, particularly as indicated by sclerotic changes in the glomeruli, were more pronounced than before spawning, although they were seldom as widespread or as advanced as those seen in the corresponding unfed salmon. The deterioration of the pancreas in the spent sockeye, especially the exocrine portion, is of some interest. Robertson and Wexler (1960) in their study of unfed spent Pacific salmon reported a diminution in the amount of exocrine tissue, but, in contrast to the findings in this study, they described the remaining zymogenous cells as being heavily granulated and normal in appearance. In addition, they found the β cells in the islets of Langerhans of the spent fish to be heavily granulated, which was seldom the case in our study.

The rapid deterioration of the pancreas, and the continuing degeneration of the kidney in the fed fish between the time of sexual ripeness and the completion of spawning, may be a reflection of the changes that occur during this period in both their feeding and behaviour patterns. A reduction in or cessation of feeding at a time of heightened sexual activity might conceivably place a

demand on the body for energy far in excess of that available from the food consumed. Whether this demand for energy would be of such a magnitude as to result in the degenerative changes noted remains a question for speculation.

An attempt was made to assess the possible role of environmental stresses in the degenerative alterations that occur in the unfed fish during sexual development. It has been pointed out in the introduction that in the wild, the starved salmon is often subjected to a variety of stresses to which they are unaccustomed. In the present study, selective removal of all fish which failed to respond to disease treatment while held in captivity as well as those which had been accidentally mishandled during the course of the study gave us some assurance that the histological changes studied were, in fact, related to the development of the gonad and not the result of external stresses. Although it is not possible to document the stresses the starved sockeye experience in the wild, the data do indicate that, with the possible exception of the pancreas, the degenerative changes that occurred in the unfed spent fish were generally more pronounced in those fish which had spawned in their natural habitat. In the pancreas the alterations were so extensive that it was impossible to make any distinction between fish spawned in captivity and in their natural habitat. It seems reasonable to associate the increases in tissue alterations with the various stresses these fish encountered while in their natural habitat.

Robertson attributes the deterioration of the tissues in the unfed sexually developing salmon to a progressive increase in the concentration of 17-hydroxycorticosteroids in the blood. In the present study a variable hyperplasia of the adrenocortical tissue did occur during sexual ripening (A. P. Van Overbeeke, unpublished data) but the change was not accompanied by an increase in the blood 17-hydroxycorticosteroid cortisol concentration (U. H. M. Fagerlund, unpublished data). Increases in the latter were evident, however, during the period of spawning. In the sexually maturing, and in the spent fish, the blood cortisol concentration seldom exceeded the low ranges noted in the sea-green sexually immature fish. Thus, it is unlikely that the degenerative changes described in the present study can be attributed to increases in the concentration of 17-hydroxycorticosteroids in the blood.

In the absence of any data on the production and concentration or the effects of the estrogens and androgens in the tissues of the fish, one can only speculate regarding the role that these or other sex steroids may play in the degenerative changes described. However, a decided increase in the number of pituitary gonadotrophs, coupled with the intense stimulation of these cells (Robertson and Wexler, 1962; A. P. Van Overbeeke and J. R. McBride, unpublished data) during the time of sexual development, suggests that this part of the endocrine system may be involved in the deterioration of the spent salmon. Investigations of the pituitary–gonad relationship are planned.

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A Hatchery Release Tank for Pink Salmon Fry With Notes on Behavior of the Fry in the Tank and After Release[1]

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ABSTRACT

A hatchery release tank was designed which permitted the voluntary release of pink salmon (*Oncorhynchus gorbuscha*) fry. Fry release was stimulated by rising temperatures and increasing turbidity. Because even relatively immature fry left the tank under these conditions, fry were released only between 0800 and 1000 hr, when both temperature and turbidity were low. After entering the stream, hatchery-produced fry appeared to behave normally. They buried themselves during daytime and, within a few days, moved downstream during the night.

INTRODUCTION

In 1957, the Fisheries Research Board of Canada established an experimental hatchery at Kleanza Creek, a tributary of the Skeena River. An important aspect of the program was the development of techniques which would permit the release of individual fry from the hatchery to the stream at the same stage of development and over the same period of time as naturally produced downstream migrants. To achieve this end, release tanks were designed to provide as nearly as possible the natural light, temperature, and other conditions characteristic of the terminal stages of normal larval development. The following is a description of the construction and use of the release tanks along with some observations on the behavior of pink salmon fry (*Oncorhynchus gorbuscha*) both in the tank and immediately after release.

DESCRIPTION OF THE TANK

The tank (Fig. 1), constructed of $\frac{3}{4}$-inch plywood, was 2 ft × 4 ft × 4 ft outside dimension. Inside, a partition 4 inches from the back wall extended from the top of the tank to a false floor of 14 × 15 mesh lumite screening. The false floor sloped downward to the front of the release tank so that any air inadvertantly introduced with the incurrent water supply moved toward the rear of the tank and escaped up behind the partition without disturbing the fry.

Water entered the release tank in two places: at the top of the partitioned space and directly beneath the front end of the false floor. The water supply

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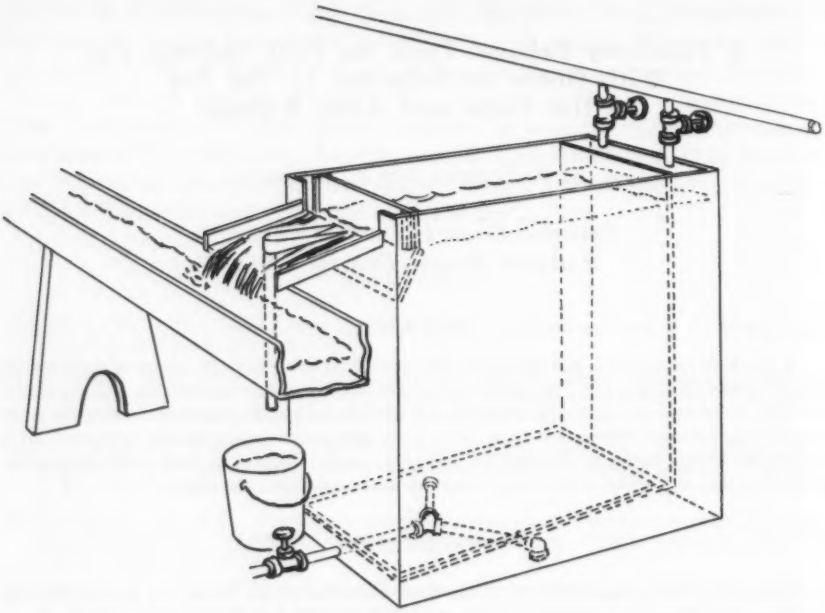

FIG. 1. Hatchery release tank for pink salmon fry.

from both sources totaled approximately 2 Imp gal per minute for every square foot of screened floor.

Upwelling water passed through the false floor into the tank and overflowed down a ramp at the top. A removable screen regulated the movement of fry down the ramp. During release periods, when the screen was lifted, a proportion of the fry moving down the ramp was sampled through a 1-inch slot in its center. Fry entering the sampling slot fell into a container below. A ratio of fry sampled to total output was established for each sampler so that an estimate of the total hatchery release could be calculated.

To reduce light to a minimum, the release tanks were covered and kept in a dark, windowless building. Work in the vicinity of the tanks was performed in the light provided by the careful use of flashlights.

TRANSFER OF FRY TO THE RELEASE TANKS

Toward the end of their larval development, when the yolk sac was almost entirely absorbed, the fry were transferred in darkness from incubating trays (patterned after those described by Burrows and Palmer, 1955) to the release tanks. Normally, fry placed in the tanks settled immediately to the bottom and remained quiescent for a period of continued development. On occasion, however, lethal oxygen depressions developed when large numbers

of excited, active fry were released into the tank at one time. Such mortalities were avoided when successive groups of fry were allowed to settle quietly to the bottom before further additions were made. By observing such precautions, as many as 200,000 fry were safely held in a single tank.

On April 26, 1960, three successive groups of 70,000, 60,000 and 50,000 fry were placed in a release tank over a period of 4 hr. The oxygen tension of the incurrent water supply averaged 13.0 ppm at a temperature of 4 C. During the 4-hr period the oxygen level dropped as low as 8.5 ppm in parts of the tank. However, 45 min after the last fry had entered, oxygen levels ranged from 10.9 to 11.9 ppm, well above lethal levels, despite the fact that 180,000 fry were confined in a very limited space.

FRY BEHAVIOR IN THE TANK

Until hatchery-reared pink fry approached the migratory stage, they remained relatively quiescent when held in complete darkness. Very few were active enough to swim up a distance of 1 ft. Exceptions to this are discussed in a later section. Better-developed fry, those in which the yolk sac was almost completely absorbed, began to swim actively off the bottom, eventually reached the surface and were swept out with the overflow into the creek. Because the eggs were incubated in water of natural temperatures pumped directly from the donor creek, it was hoped that the rate of development and, therefore, the time of appearance of behavior patterns associated with downstream migration would be similar for both hatchery- and naturally produced fry.

PERIODICITY OF RELEASE

Figure 2A illustrates the periodicity of voluntary fry release over a typical 24-hr period. In this, as in most instances, the number of fry leaving the release tank was directly related to the water temperature. The numbers, low in the morning, increased steadily until midafternoon, the period of maximum water temperature, and dropped again to low levels during the coldest parts of the night. This pattern was presumably related to a temperature-induced increase in the vertical swimming activity of fry in the release tanks. During the warmest hours of the days even relatively immature fry were found near the surface of the tank.

On occasion, water turbidity also appeared to stimulate vertical swimming activity and fry release. On warm spring days melting snow rapidly raised the level of the creek and the water circulating through the release tanks became muddy. In these circumstances (Fig. 2B), large fry releases occured even when water temperatures were declining. After an initial spurt, immediately after the tank was opened, the timing of release followed the usual temperature-related pattern. There was a gradual increase up to 1700 hr, when the maximum water temperature was reached, followed by a decline coincident with declining water temperatures. However, even though temper-

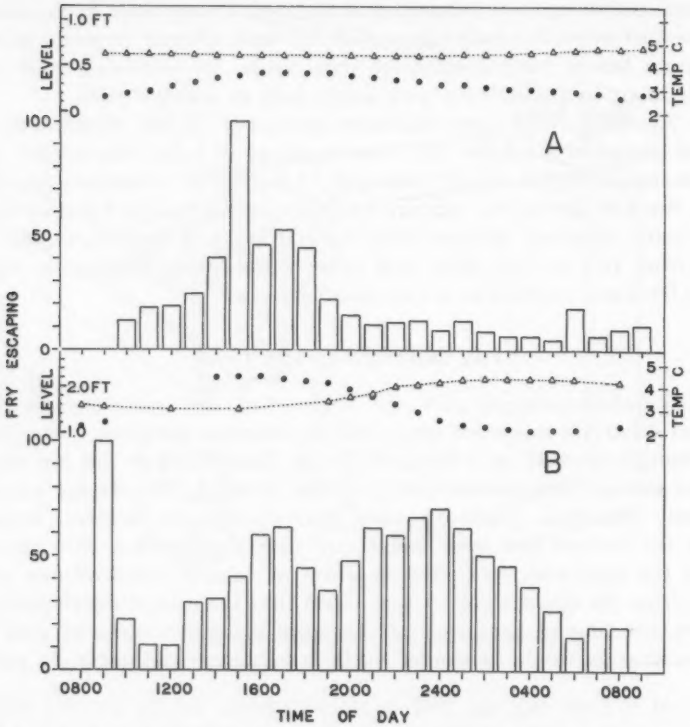

FIG. 2. Periodicity of voluntary release of pink fry on two different occasions. Hourly fry escapements are given as percentages of the largest single 1-hr release during the period of observation. Triangles indicate the water levels, and circles indicate the water temperature in the creek.

atures continued to decline, fry releases began to increase again after 1900 hr up to a peak at 2400 hr. The fact that water levels in the release tanks were constant suggests that the increased release was primarily an effect of changing water quality, presumably the heavy silt load. Two experiments performed at the Research Board's Scully Creek hatchery support this view. These experiments (Fig. 3) were performed with sockeye salmon. (*O. nerka*) fry but in this instance the two species probably behave similarly.

In these experiments a mixture of water and fine slit of the same temperature as the hatchery water supply was introduced into one or the other of two release tanks, miniaturized versions of the standard hatchery tanks. Half-hourly counts were made both before and after the introduction of the mixture.

In most instances the addition of silt resulted in an immediate increase in fry output followed by a rapid decline. On one occasion, however, (experi-

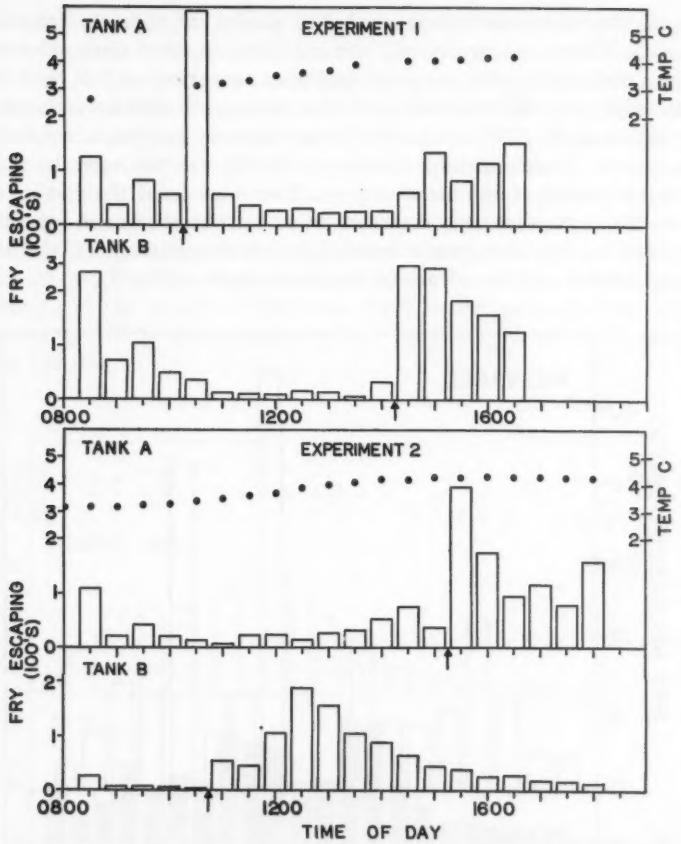

FIG. 3. Periodicity of sockeye fry release from paired experimental tanks in two experiments. The arrows indicate the time at which silt was introduced into the incurrent water supply. Note the change in scale at fry releases in excess of 200.

ment 2, tank B) counts continued to increase for several hours after the addition of silt.

Silt, like rising temperatures, stimulated the release of many relatively immature fry with large yolk sacs. To keep the incidence of such fry in releases to a minimum it became standard practice to open the tanks for only a short period between 0800 and 1000 hr, when both temperature and turbidity were normally low and only the most mature fry were highly active.

BEHAVIOR OF FRY AFTER RELEASE

In the Skeena River system, the downstream migration of naturally produced pink salmon is almost entirely nocturnal. The fry hide in the gravel

during the day and move off the creek bed during the night to emigrate from the stream. There was no known natural production of pink salmon fry in Kleanza Creek during the years of hatchery operation and it was therefore possible to observe the behavior, in the stream, of hatchery-produced fry.

It appeared that fry released from the hatchery exhibited natural behavioral responses. Those entering the stream during the day soon buried themselves in the stones of the creek bottom. They rose from the gravel at night and moved downstream in a manner similar to that of natural fry. The nocturnal catch of fry at trapnets located ½ mile downstream of the hatchery closely paralleled the fry release of the previous day (Fig. 4).

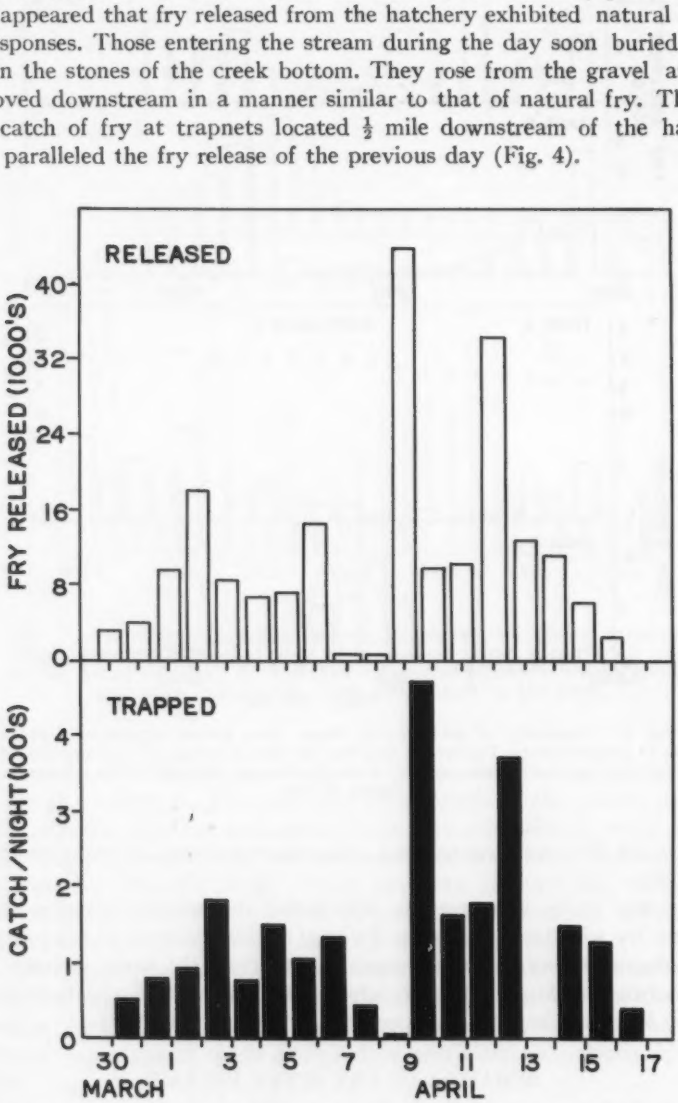

FIG. 4. Daily release of pink salmon fry from Kleanza Creek Hatchery during 1959 and the nocturnal catch of fry at traps located ½ mile downstream.

Figure 5 illustrates the release and downstream movement of fry over a typical 24-hr period, April 13 and 14, 1959. The hatchery escape followed the diurnal change in creek temperature, increasing steadily from early morning to late afternoon and then dropping to a low level at night. Fry entering the stream during the day tended to burrow in the gravel but, because many fry were swept a short distance downstream before being able to do so, a trap operated only 50 ft below the hatchery outlet caught substantial numbers throughout the day. An examination of the creek bed during the day revealed numerous fry hiding under rocks and other bottom material. Although an occasional solitary fry was seen, no schools were located anywhere between the hatchery and the mouth of the creek, 2500 ft downstream. Two series of traps located at 550 ft downstream and at the creek mouth took very few fish during the day.

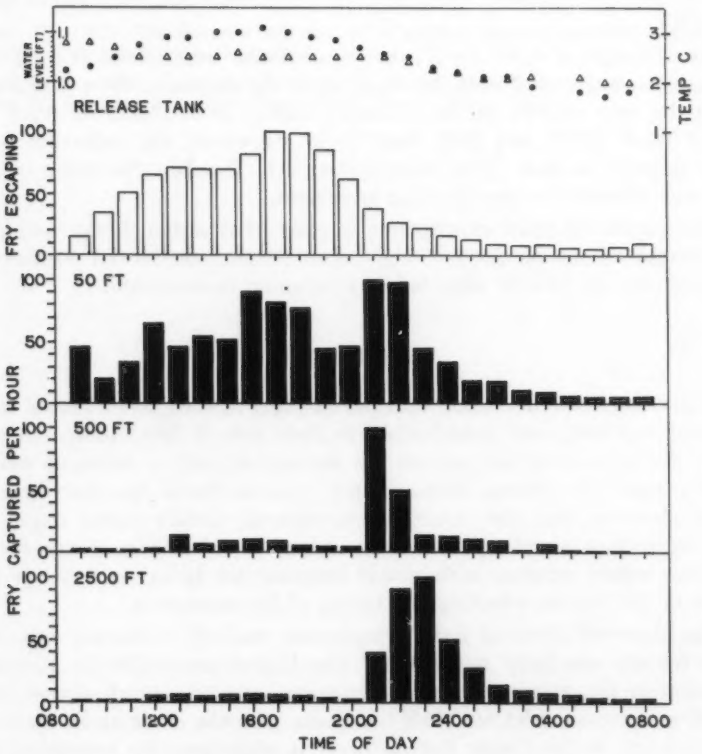

FIG. 5. The hourly periodicity of voluntary release of pink fry and of captures at traps located at intervals downstream, April 13 and 14, 1959. Hourly fry release and captures are each given as a percentage of the largest single 1-hr count during the period of observation.

As darkness approached (2030 to 2100 hr) fry moved off the stream bottom and moved downstream. From 2100 to 2400 hr all three sets of traps made large catches. There was a definite time lag between the peak catches at 550 ft and those at 2500 ft, presumably the time it took for fry to travel the intervening 1950 ft.

Although it appeared that the majority of fry moved down the creek the first night after release, it was possible that some fry remained buried in the creek for several days before continuing on downstream. Between April 23 and April 27, 1960, a series of observations was made to determine whether this did, in fact, occur.

At 1700 hr on April 23, 5000 fry marked with neutral red dye were released at the hatchery outlet. Of these, 270 were recaptured in a series of three traps situated at the creek mouth, 2500 ft downstream: 265 (98%) the first night after release and five (2%) over the following 2 days. No marked fry were recaptured thereafter although the traps were operated up to 0700 hr April 27th.

On the night of April 24/25, the release tanks were closed at 2400 hr and were not reopened until 0845 hr, April 27th. As expected, there was a reduction in the trap catches on the following nights: from 14,455 on April 24/25 to 4814 April 25/26 and 3101 April 26/27. However, the reduction was not nearly as great as that of the dye-marked fish. Possibly the behavior of the latter was affected by the marking treatment.

The results of these experiments suggest that although the majority of fry leave the stream on the first night after release, substantial numbers may remain hidden for several days before continuing downstream.

DISCUSSION

It is a common observation that the offspring of even single female salmon, incubated together, vary considerably in their rate of development. A release tank of the type described permits the separation, with a minimum effort, of those fry ready for release. Although fry from the tanks described here were released directly into the natural environment, similar tanks might have useful application where fry are being released into hatchery ponds for feeding. Miniaturized versions with gravel bottoms are being used in an investigation of the factors affecting the timing of fry emergence.

The observed effects of water temperature and silt on the activity of pink salmon fry are especially noteworthy. The factors responsible for day-to-day fluctuation in the emergence and downstream movements of salmon fry are not well understood. McCart (1967) suggests that the downstream movement of sockeye fry in the Upper Babine River is stimulated by increasing water temperatures but such a relationship has not otherwise been described. A correspondence between high turbidity and large downstream movements has been frequently observed (for instance, Withler, 1952) but this is the first

indication that the presence of silt, in itself, may be an important factor encouraging emergence and downstream movement aside from the gravel scouring, reduced visibility, and low-light intensities which usually accompany turbid conditions. Emergence during periods of turbid water conditions has a probable advantage to fry in that the efficiency of those predators which hunt by sight must be considerably reduced.

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Relationship of Temperature to Total Annual Growth in Adult Smallmouth Bass[1,2,3]

By Daniel W. Coble

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ABSTRACT

Total yearly growth of smallmouth bass, *Micropterus dolomieui* Lacépède, of ages 3–5 in South Bay, Lake Huron, and in several other widely scattered populations was related to mean surface water temperature for the period July through September, more growth being associated with warmer waters. No such relationship was demonstrated for bass of the same ages in Lake Opeongo, Ontario, nor for older bass in Lake Opeongo and South Bay. The difference in the manifestation of a growth–temperature relationship appears to be real, rather than a result of differences in data or treatments of them, and indicates, therefore, that other factors may influence total annual growth as much as, or more than, temperature.

RÉSUMÉ

La pousse annuelle totale de *Micropterus dolomieui* Lacépède de 3–5 ans à South Bay, Lac Huron, et dans plusieurs autres populations largement dispersées s'était rapportée à la moyenne de la température de l'eau à la surface pendant la période de juillet à septembre compris, en associant plus de croissance avec des eaux plus chaudes. On n'avait pas constaté de tel rapport à l'égard des bars des mêmes ages dans le Lac Opeongo, Ontario, ni à l'égard des bars plus anciens dans le Lac Opeongo et South Bay. La différence dans la manifestation d'un rapport entre la croissance et la température paraît être vraie, plutôt qu'apportée par les différences dans les données ou leurs traitements, donc elle indique que d'autres facteurs peuvent influencer la pousse annuelle totale autant que, ou plus que, la température.

INTRODUCTION

Factors which may affect growth of fish are environmental temperature, quantity and quality of food, space limitations, the light cycle, diseases, parasites, and pollution. The various factors may interact altering the effects of each other, and their effects may not be the same on fish of different ages. Frequently attempts to discern a relationship between growth and any single factor are not successful, and in some cases, a relationship between growth and some factor is found for one population and not for another of the same species.

The purpose of this study was to find out if total annual growth of smallmouth bass, *Micropterus dolomieui* Lacépède, is related to temperature and,

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if so, what variation around that relationship exists. Two kinds of information were used. One consisted of original data on two populations of smallmouth bass in Ontario for which rather detailed information on growth and temperature were obtained and treated in the same manner. The other consisted of published data on growth of smallmouth bass in various waters throughout the North American range of the species for which information on temperature could be obtained.

There is evidence that growth of smallmouth bass is related to temperature. Watt (1959) back calculated lengths and weights from scale measurements of bass in South Bay. He calculated temperature indices by taking the algebraic sum of air temperature deviations from the long term mean for the months June through October. He found significant correlations between such temperature indices and growth in weight of bass in their second and third years of life, but not for bass in their first, fourth, and fifth years of life. Latta (1963) found that growth of smallmouth bass at Waugoshance Point, Lake Michigan, was much below average in 1950 and 1951, years in which air temperatures there in July and August were below normal.

METHODS AND SOURCES OF INFORMATION

Two Ontario Smallmouth Bass Populations

Comparable information on growth and temperature were obtained for smallmouth bass found in South Bay, an 85.5 km^2 arm of Lake Huron extending into the southeast corner of Manitoulin Island; and in Lake Opeongo, a lake of about 52 km^2 lying approximately 274 km east of South Bay in Algonquin Park. Both waters are described in more detail by McCombie (1959), and the South Bay bass fishery by Fraser (1955).

McCombie (1959) showed linear relationships between air and water temperatures for various months in three bodies of water including South Bay and Lake Opeongo. His regression equations were used to obtain water temperatures from air temperatures.[4] Air temperatures were obtained from the Monthly Records of the Meteorological Branch of the Canadian Department of Transport and from Dr McCombie (personal communication). Mean temperatures were calculated for each of the months of July, August, and September for the years 1949 through 1963 in South Bay, and 1947 through 1962 in Lake Opeongo. Temperature data for the month of June were not included because McCombie's data did not allow him to determine a reliable regression of water temperature on air temperature for that month in Lake Opeongo. Since an attempt was being made to obtain completely comparable information for the two bodies of water, June temperature data were omitted for South Bay too.

[4]The values of intercept in McCombie's Table 1 are not correct for the values of slope given. However, these constants may be used after first converting the values for intercept to Fahrenheit and using Fahrenheit for the air temperature value in the equation. A copy of the corrected table may be obtained from Dr McCombie at the address given in footnote 2.

The air–water temperature relationships in Algonquin Park were established by McCombie (1959) for air temperatures at Cache Lake and water temperatures in Lake Opeongo. Beginning in 1960, air temperatures were no longer recorded at Cache Lake; hence, for the purposes of this investigation, it was necessary to estimate Cache Lake air temperatures from 1960 on. Air temperatures have been recorded at Cache Lake and at Killaloe, a station 97 km to the east for 22 years before 1960, and continuing at the latter station up to the present. Regression equations describing the linear relationships of Cache Lake and Killaloe air temperatures were determined for the 22 years preceding 1960. The equations, July, $y = -1.5 + 1.004\,x$; August, $y = -0.105 + 0.989\,x$; September, $y = 4.395 + 0.903\,x$, were used to calculate Cache Lake temperatures (yF) from Killaloe temperatures (xF) for the later years.

Creel censuses of the smallmouth bass fisheries in South Bay and Lake Opeongo have been carried on for many years. In the censuses fish were measured and scales were taken. Age determinations from the scales have been made by several experienced scale readers, and data on average lengths of bass at various ages in the various years have been compiled. Annual growth was determined from these data by subtracting mean lengths of bass of age n in year p from mean lengths of fish of age $n+1$ in year $p+1$.

The accuracy of such calculations of length increments depends on the two mean lengths, whose accuracies depend on the number of observations (samples sizes) from which they were calculated. Of the two samples, the smaller is most important in limiting the reliability of the final figure of length increment. For example, if the mean length of 50 4-year-old fish is 10 inches, and in the following year, one 5-year-old fish measuring 11 inches is captured, it can be said that the fish grew an.inch in the year. But the reliability of the 1-inch increment depends on one observation to a greater extent than on the 51 observations.

The calculated length increments were combined (pooled) for each year for bass between ages 3 and 4, and 4 and 5, and for fish between ages 5 and 6, and 6 and 7; and for bass between ages 7 and 8, 8 and 9, and 9 and 10, if a sufficient number of the older fish were captured. Before the length increments were pooled, each was weighted by the smaller of the two sample sizes on which its accuracy depended. For example, in South Bay, for 1949, the mean length increment of bass between ages 3 and 4 was 1 inch and its realibility depended most heavily on 52 observations. The 1 inch was multiplied by 52. Similarly, 1.2 inches, the mean length increment of bass between ages 4 and 5, multiplied by 18, the smaller of the two samples of fish of those ages, equals 21.6. Then $(52 + 21.6)/(52 + 18)$ is equal to 1.05 inches, the weighted pooled length increment of bass between ages 3 and 5 for South Bay for 1949. The weighted pooled length increments and the weights are shown in Tables I and II.

It was necessary to make a correction in the weighted pooled length increments for fish in the youngest age-grouping (3–5) in some years. A minimum legal length of 10 inches fork length (11 inches total length in 1955) was opera-

TABLE I. Calculated mean water temperatures, average annual length increments and their weights (*n*) for smallmouth bass in South Bay.

Year	Temp (*C*)	Length increments (*inches*)						
		3–5	Corrected[a]	*n*	5–7	*n*	7–10	*n*
1949	17.4	1.05	1.49	70	0.86	59	0.65	23
1950	16.6	0.60	0.85	147	1.15	20	0.37	15
1951	17.6	1.08	1.53	241	1.46	40	0.92	13
1952	18.2	1.09	1.55	197	1.19	297	–	–
1953	18.0	0.80	1.14	119	0.97	249	–	–
1954	18.4	–	–	–	1.20	523	1.11	52
1955	17.8	0.51	0.72	109	1.38	111	1.06	36
1956	17.0		0.94	594	1.59	19	1.03	56
1957	17.3		0.93	204	1.01	195	0.51	19
1958	17.9		1.17	423	1.60	180	1.30	24
1959	18.2		1.10	934	1.56	35	–	–
1960	18.0		1.46	154	1.39	337	0.95	23
1961	18.5		1.72	286	1.59	181	0.57	13
1962	17.7		1.19	707	1.09	23	0.91	27
1963	17.8		1.21	245	1.48	10	0.41	11
Sum				4430		2279		319
Mean[b]	17.8		1.21		1.30		0.82	
SD[b]			0.30		0.25		0.30	

[a]The correction, which is explained in the text, increases the calculated increments of the younger bass caught in the angling fishery in years when a legal size limit was in effect to make them comparable with the increments in later years.
[b]Not weighted.

tive until 1956, and in that and later years no size limit was imposed. Many smallmouth bass do not attain a length of 10 inches at ages 3 and 4 in South Bay (Fraser, 1955) and Lake Opeongo (Christie, MS, 1957). Catches of bass from 1956 on contained all sizes of fish of ages 3 and 4, whereas in the earlier years, only the larger bass of those ages could legally be retained. Therefore, average lengths of fish in the 3–5 age-group were higher in the earlier years resulting in smaller calculated length increments before 1956.

The mean of the weighted pooled length increments of South Bay bass from 1949 through 1955 was 0.85 inches, and the analogous average increment from 1956 through 1963 was 1.21 inches. The ratio of the mean for the later period divided by the mean for the earlier was 1.42. The mean increment for each year from 1949 through 1955 for South Bay fish of age group 3–5 was multiplied by 1.42 to make the growth data for the earlier period comparable with that of the later one. Similarly, a ratio of 1.52 was obtained for growth of Opeongo bass of age-grouping 3–5. Length increments for each year from 1947 through 1955 were multiplied by the factor to correct them to figures comparable to the later years.

The original increments obtained by subtraction of mean lengths of bass of successive ages in successive years were calculated from mean lengths of

TABLE II. Calculated mean water temperatures, average annual length increments and their weights (n) for smallmouth bass in Lake Opeongo.

Year	Temp (C)	Length increments (*inches*) 3–5	Corrected[a]	n	5–7	n
1947	20.1	0.83	1.26	37	1.57	54
1948	19.9	0.80	1.22	196	0.67	75
1949	18.8	0.37	0.56	56	1.25	34
1950	18.5	0.78	1.19	79	1.38	30
1951	19.1	0.32	0.49	68	0.50	28
1952	19.4	0.53	0.81	18	0.86	35
1953	18.8	1.30	1.98	48	1.44	62
1954	19.2	0.93	1.42	14	0.52	203
1955	19.2	0.20	0.30	151	0.81	97
1956	18.6		0.90	268	1.46	25
1957	18.4		0.77	86	1.38	43
1958	19.3		0.67	130	0.91	38
1959	19.6		1.03	228	1.06	21
1960	19.1		1.91	40	0.79	185
1961	18.7		1.09	64	1.54	84
1962	18.9		0.81	309	1.04	32
Sum				1792		1046
Mean[b]	19.1		1.03		1.07	
SD[b]			0.47		0.36	

[a]See footnote in Table I.
[b]Not weighted.

fish of certain ages in certain years. Such lengths represented averages of fish caught throughout the fishing season. They were not average lengths of fish at the beginning or end of the season, but at a point in between depending on when the bass were caught. It was assumed that the mean lengths of bass at each age represented the average length of the fish at about midsummer, the end of July. Therefore, the increments obtained by subtraction of mean lengths would not represent growth throughout a calendar season, but instead from the end of July in one year to the end of July in the next year. Accordingly, the weighted pooled length increments for year p were compared with the means of calculated water temperatures for August and September in year p and July in year $p+1$. The temperatures given for each year in Tables I and II, then, are means of the mean temperatures for August and September of that year and July of the next year.

SOME OTHER SMALLMOUTH BASS POPULATIONS

Below are listed sources of information on growth of smallmouth bass in other populations along with the source of temperature data pertinent to each. All data on growth were treated as above, to yield mean weighted increments between ages 3 and 5. In general, temperatures too were weighted by the number of days to which they referred, e.g. a mean monthly temperature would be

given 30 or 31 times the weight of a single daily temperature, and were used to calculate a mean surface water temperature for July through September.

DOAN, K. H. 1940. Growth calculated for fish taken in Lake St. Clair in 1935 and 1936 by angling and by fyke nets. Temperatures obtained from Station 62 of Millar, F. G. (1952) which covered the period 1937–1941. Temperature data supplemented by seven individual daily recordings taken from cruises of the C.M.S. *Porte Dauphine* in 1960–1962 and reported in Data Reports of the Great Lakes Institute, Univ. of Toronto, Preliminary Rept. Nos. 11, 3, 16.

1940. Growth calculated for bass taken in the vicinity of the Bass Islands in western Lake Erie in 1938. Temperatures from Station 63 of Millar, F. G. (1952) were supplemented by 18 daily temperatures obtained and reported as above.

1940. Doan's data on lengths and ages of bass taken from eastern Georgian Bay in 1936 were supplemented substantially by unpublished data from fish taken by angling and trap nets in the vicinity of Parry Sound, Ontario, in 1960 through 1964. Temperatures were obtained from Station 50 of Millar, F. G. (1952) which covered the period 1936–1939 and 1941 and from thermograph records from the Western Islands in 1963 and 1964 and from 20 daily temperatures taken from the C.M.S. *Porte Dauphine* in 1961 and 1962 which were reported in Preliminary Rept. Nos. 4 and 17.

1940. Growth calculated for smallmouth bass caught in Cache Lake and the Madawaska River, Ontario in 1935–1937. Temperatures obtained from records of the Ontario Dept. of Lands and Forests, for the years 1947–1949.

HENDERSON, C., AND R. F. FOSTER. 1956. Growth calculated from data in Fig. 3 that consisted of lengths and ages of smallmouth bass caught in 1952 in the Columbia River near Hanford, Washington. Temperature data in the paper were supplemented by data taken at the Grand Coulee Dam, Washington, and from the river at Maryhill Ferry near Rufus, Oregon which were reported in U.S. Geological Survey Water-Supply Paper 1200. Quality of Surface Waters of the U.S. 1951, U.S. Government Printing Office, Washington, D.C. The Hanford area is about halfway between Grand Coulee and Maryhill Ferry.

BISHOP, S. C. 1935. Data on p. 127 used to calculate growth of bass caught in 1935 in the Delaware River. Temperatures at Narrowsburg, N.Y. in 1949 from Water-Supply Paper 1162 were averaged with those at Port Jarvis, N.Y. in 1957 through 1959. The latter were obtained from Mr Ralph C. Heath, District Chief, U.S. Geological Survey, Albany, New York.

SURBER, E. W., AND E. A. SEAMAN. 1949. Information on growth of angled bass from the South Branch of the Potomac River near Romney, West Virginia in 1936, 1938, 1947, and 1948, and from the Cacapon River near Capon Bridge and Largent, W.Va., in 1938, 1947, and 1948, and from the Shenandoah River near Berryville, Virginia, in 1935 was taken from Tables 8–13. Temperatures

in the South Branch of the Potomac River at Romney W.Va. in 1952, 1954, 1955 and in the Cacapon River at Great Cacapon, W.Va. in 1947, 1948, 1949, 1954, and in the Shenandoah River at Front Royal, Va. in 1954, 1955, and at Strasburg, Va. in 1949 were obtained from Water-Supply Papers 1102, 1132, 1162, 1350, and 1400.

LATTA, W. C. 1963. Growth calculated from length and age data in Table 9 for smallmouth bass caught in trap nets at Waugoshance Point, Lake Michigan in 1953–1955. Temperatures from Station 38 of Millar, F. G. (1952) covered the period 1935–1941.

BENNETT, G. W. 1938. Growth of smallmouth bass in Nebish Lake, Wisconsin, was calculated from length and age data in Table 2. The temperature data that were readily attainable consisted only of four daily observations in 1964.

SANDERSON A. E., JR. 1958. Growth of bass collected by electro-fishing in 1955–1957 in the Potomac River in Allegany County and Bennett Creek, Maryland, was calculated from data in Table 1. Potomac River temperatures at Hancock, Md., in 1954 and 1955 were taken from Water-Supply Papers 1350 and 1400. Miscellaneous temperatures (19 for the July–September period) from Bennett Creek at Park Mills, Md., within the period 1948–1958 were obtained through the kindness of Mr L. M. Lenfest, U.S. Geological Survey, Water Resources Division, College Park, Md.

PATRIARCHE, M. H., AND E. M. LOWRY. 1953. Data on growth of smallmouth bass captured in the Black River, Missouri, in 1947 and 1948 are contained in Table 2. Temperatures at Black Rock, Arkansas, in 1946 were obtained from Water-Supply Paper 1050.

PATRIARCHE, M. H., AND R. S. CAMPBELL. 1957. Data on growth of bass taken in various kinds of nets in Clearwater Reservoir, Missouri for the period 1948 through 1952 are given in Table 3. Temperatures recorded in 1952 and 1953 were obtained through the efforts of Dr Robert S. Campbell, Professor of Zoology, University of Missouri, Columbia, Mo.

STROUD, R. H. 1948. Information on growth of smallmouth bass in Norris Reservoir, Tennessee, averaged over the period 1936–1945 was obtained from Table 7. Temperatures occurring within the period 1937–1944 were obtained through the kindness of Mr James W. Beverage, Chief, Hydrolic Data Branch, TVA, Knoxville, Tenn.

For the first four papers mentioned above, growth was calculated from average sizes of fish at various ages, and these data are quite similar to those for South Bay and Lake Opeongo. In the remainder of the sources, average lengths were originally calculated from scale measurements. In the latter group, a length increment between ages 3 and 4 would involve only the increment between the formation of the third and fourth annuli. In the former

group, only part of the increment (at least $\frac{2}{3}$ in South Bay) occurred between the formation of these two annuli. The same would apply for the other annuli. Although the two increments are not entirely comparable, they were considered so in this study.

The reason for the selection of mean surface water temperature for the period July through September as the measure of environmental warmness was given above in connection with the South Bay and Lake Opeongo populations. The same statistic was calculated for the other bass populations. In the northern part of the range, temperatures that are not attained until July may have been reached and exceeded in the southern part of the range months earlier, indicating that the statistic may not be appropriate for use over a wide range of latitude. Perhaps a better statistic would be thermal sums above a base of say, 10 C. For each of the smallmouth bass populations for which the available temperature data were extensive enough, the number of degree-days above 10 C was calculated. These thermal sums are given in Table III along with the mean surface water temperatures for July through September and the weighted pooled length increments and their weights for the various waters. The linear relationship between the mean temperatures and thermal sums may be expressed by the equation, $y = -2837 + 210\ x$, where x is the mean temp-

TABLE III. Mean surface water temperatures for July through September, thermal sums above 10 C, average annual length increments and their weights for various populations of smallmouth bass.

Body of water	Temp (C)	Thermal sums degree-days	Length increments	
			3–5	*n*
Eastern Georgian Bay, Ontario	17.4	886	0.57	225
Columbia River, Washington	17.5	848	0.84	33
South Bay, Lake Huron	17.8	1046	1.21	4430
Waugoshance Point, Lake Michigan	17.9	869	1.36	2962
Nebish Lake, Wisconsin[a]	18.5	–	1.25	?
Lake Opeongo, Ontario	19.1	1081	1.03	1792
Cache Lake and Madawaska River, Ontario	20.9	–	1.49	74
Lake St. Clair	21.3	1769	1.45	138
Bennett Creek, Maryland[a]	22.0	–	0.65	?
Western Lake Erie	22.0	1572	1.71	150
Delaware River, New York	22.7	1794	0.38	23
Black River, Missouri	23.1	2279	2.58	43
Cacapon River, West Virginia	23.4	1958	1.15	80
South Branch Potomac River, West Virginia	23.5	2036	1.29	115
Shenandoah River, Virginia	25.2	2545	1.84	49
Potomac River, Maryland[a]	25.5	2380	1.80	?
Clearwater Reservoir, Missouri	26.6	2800	2.55	35
Norris Reservoir, Tennessee	27.8	3100	2.02	202

[a]It was not possible to determine the sample size pertaining to each age-group in the papers of Bennett (1938) and Sanderson (1958). Judging from the number of bass caught in each study samples probably did exceed 10 fish in the 3–5 age-group, the arbitrarily selected lower limit of sample size for this study.

erature for July–September and y is the degree-days above 10 C. The correlation coefficient is 0.984. It appears, therefore, that the mean temperature for July through September is a satisfactory measure of environmental warmness.[5]

RESULTS

For smallmouth bass of ages 3–5 in South Bay and in the various waters enumerated above, there was a relationship between total annual growth and temperature, more growth being associated with warmer waters (Fig. 1). There was no demonstrable growth–temperature relationship for bass of the same ages in Lake Opeongo nor for the older fish in South Bay and in Lake Opeongo. Regression equations were calculated for each of the groups of growth–temperature data, and the values of slope and intercept of the equations are given in Table IV along with values of r^2, the coefficient of determination.

TABLE IV. Values of the coefficient of determination, r^2, and of the constants for slope and intercept of linear equations expressing the relationships of length increments to temperature. Slopes are significant for bass of ages 3–5 in South Bay and in the various localities (F-test; 95% level).

Location	Age-group	r^2	Slope	Intercept (*inches*)
South Bay	3–5	0.313	0.329	–4.615
	5–7	0.060	0.117	–0.786
	7–10	0.123	0.196	–2.653
Lake Opeongo	3–5	0.005	0.067	–0.254
	5–7	0.128	–0.269	6.210
Various sources	3–5	0.362	0.114	–1.079

The values of r^2 show that in the younger bass in South Bay and in the various waters, more than 30% of the variation in the data is attributable to temperature whereas less than 1% of the variation in the data for smallmouth bass of ages 3–5 in Lake Opeongo is attributable to temperature. The strength of the relationship for the younger fish in the several populations is striking in view of the many sources of error that were possible in that analysis. For the older smallmouth bass, only about 10% of the variation in the data was attributable to temperature.

The coefficient of determination, it should be appreciated, is an algebraic identity concerning only the data used in its calculation. It would seem that if better information were available, e.g. growth of fish during a specific period and water temperatures recorded in the habitat of the fish in the same period,

[5]The thermal sum for South Bay represents a 10-year average for the inner basin of South Bay for the period 1953–1962, which was not available at the time the regression was calculated, and, therefore, was not used in calculating the equation or the correlation coefficient.

higher values of r^2 could be obtained. A value of 30–35% of the variation in growth of smallmouth bass of ages 3–5 attributable to temperature may be a minimal figure.

DISCUSSION

These data have been treated in ways to show the relationships of growth to temperature. There is a good deal of variation in the data, and it must be attributed to errors and to factors other than temperature that influence growth. Sampling error must be present in the data, but it probably does not account for the different results. With older fish both smaller samples and greater variation in growth are frequently encountered. Yet the values of standard deviation of the length increments at the bottoms of Tables I and II indicate no greater variability in the data for older fish. There is more variation in the length increments in Lake Opeongo than in South Bay, which may be related to the smaller samples from the inland lake; however, none of the variances in increments were significantly different (F-test; 95% level) when compared between age-groupings in each body of water or between waters within age-groupings.

Although growth-affecting factors other than temperature were not measured, they probably should be considered to emphasize their possible roles in altering and even masking a growth–temperature relationship. The information shown in Table IV and Fig. 1 indicates that such a relationship does exist in

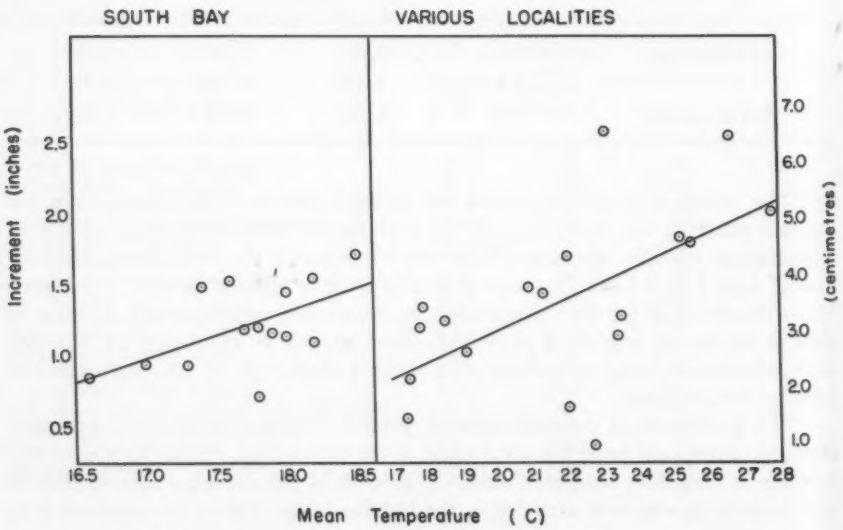

FIG. 1. Annual length increment of smallmouth bass of ages 3–5 in South Bay, Lake Huron, and in various populations enumerated in the text in relation to mean surface water temperature for the period July through September. The slopes of the regression lines, which are placed by the method of least squares, are significantly different from zero (F-test; 95% level).

smallmouth bass of ages 3–5. An attempt was made to obtain comparable data for these fish in Lake Opeongo and South Bay by treating the same kind of information in the same manner. If the data are comparable, the difference in the manifestation of a growth–temperature relationship indicates a real difference between smallmouth bass of ages 3–5 in these two populations. Not only does growth in relation to temperature differ, but also the amount of annual growth. The values of mean length increment at the bottoms of Tables I and II show that smallmouth bass in Lake Opeongo do not grow as much in a year as those in South Bay. Hence, even though Lake Opeongo is warmer than South Bay, conditions conductive to growth of the younger bass apparently are not so good.

Lake Opeongo lies in the Precambrian shield of Ontario, whereas South Bay has a limestone watershed. The waters of South Bay, then, can be expected to be richer in nutrients (Ryder, 1964, 1965). Such a difference in water quality could affect growth of smallmouth bass by influencing the food supply. Stanislav (1964) and Langford and Martin (1940) related growth of fish to food conditions. Smallmouth bass in Lake Opeongo are subject to more parasitism than those in South Bay, and they bear exceptionally heavy parasite loads (personal communication, Dr A. Dechtiar, parasitologist with the Ontario Department of Lands and Forests; Bangham, 1940). Heavy parasite loads may be detrimental to growth of smallmouth bass (Van Oosten, 1944). These differences between South Bay and Lake Opeongo are only two of the more obvious ones that could account for the apparent differences in growth and in growth in relation to temperature for the younger fish in the bass populations.

In contrast to this situation the difference in the results of Watt (1959) and those presented here for the younger South Bay bass are likely not real. Watt (1959), as was mentioned in the Introduction, did not find a growth–temperature relationship for South Bay bass in their fourth and fifth years of life (ages 3 and 4 respectively) whereas in this study fish of those ages in South Bay showed a strong growth–temperature relationship. The difference in the results of the two studies is probably attributable to differences in the data used. The number of years of data available to Watt was less than was used here, and his temperature indices (which he called crude) may not have reflected South Bay temperatures so precisely as the temperature data of this study.

It appears that factors other than temperature are more important in influencing total annual growth in older smallmouth bass than in the younger fish. Such a conclusion is supported by the lack of a demonstrable growth–temperature relationship in the older bass and by the low values of the coefficient of determination. A difference in the role of temperature in affecting growth according to age (hence, size) is reasonable in view of the differences which may exist between fish of different ages, such as metabolic rate, diet, and habitat. Indeed, the higher metabolic requirements of larger fish (Beamish, 1964; Job, 1955) suggest that food supply would be of more relative importance to them. However, in view of the lack of quantitative information on the food supply and on other potential growth affecting factors, as well as the lack of infor-

mation on age specific differences in behaviour in smallmouth bass, further discussion of these aspects does not seem warranted. It appears that improved understanding of total annual growth in smallmouth bass, and in other species too (Coble, 1966), will require that information be obtained simultaneously for not one, but several possible growth-influencing factors.

ACKNOWLEDGMENTS

The part of this study concerning South Bay and Lake Opeongo, which was initiated through the encouragement of Dr F. E. J. Fry, would have been impossible without accurate age determinations and data tabulations that have resulted from the efforts of many people including Mmes G. W. Bennett and E. Jermolajev, Messrs R. Christie, W. J. Christie, J. M. Fraser, A. Kaufman, J. B. Smith, Dr K. E. F. Watt, and the late Hartley Holmberg. The part of it concerning other waters was accomplished with the cooperation of even more people, some of whom were put to some inconvenience to provide the data that I requested. They are not named here only because the list would be too long. Dr J. C. MacLeod made much of the Lake Opeongo data available and offered helpful suggestions. He, along with Mr W. J. Christie, Director of the Glenora Fisheries Station, and Dr W. E. Ricker, read the mauscript. Mr John Dobell drew the figure.

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The Thermal Regime of South Bay, Manitoulin Island[1,2]

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ABSTRACT

The thermal regime of South Bay is described from records collected from 1953 to 1962 with thermometers, thermographs, and bathythermographs, the last being cast at 11 stations along the bay and one in Lake Huron .Warming begins in April and thermal stratification is established in June. Shallow areas warm more rapidly than deep in the spring and cool more quickly in autumn. The boundary between the epilimnion and the thermocline becomes sharper as summer advances but the transition from thermocline to hypolimnion remains gradual. The average seasonal trend of surface temperatures is a sine function with a maximum of 66 F in mid August and a minimum of 34 F in late March, though values outside this range occur frequently. At 180 ft the maximum of 47 F is attained in November. At the lake and outermost bay stations there is a temperature slump in June and July which may be due to an upwelling in the lake. Evidence of an exchange of water between the lake and bay is seen in vertical temperature sections and water movements Variations in epilimnial temperatures are correlated with those of the air temperature, but variations in epilimnial and hypolimnial temperatures appear to be unrelated. Finally, literature describing the influence of temperature on the year class strength of smallmouth bass, the distribution of lake trout, the growth of yellow perch, and the life history of *Pontoporeia* in South Bay is reviewed.

INTRODUCTION

Since 1947, when the Ontario Department of Lands and Forests established a fisheries research station on South Bay, Manitoulin Island, records have been kept of the local weather conditions and water temperatures as a part of a study of the physical environment. The purpose of this report is to summarize the water temperature records for the decade 1953 to 1962, to describe some of the salient features of the thermal regime of the bay and to consider some of the ways in which that regime might affect the fish populations.

The general features of the regime are outlined first and then some of the variations which have occured from one year to another are discussed. Among the features described are the changes in temperature with season, depth, and location along the major axis of the bay. Note is also taken of the times of year when the water begins to warm, when the thermal stratification is established, when the maximum temperature is attained, when fall cooling commences, and when the vertically isothermal condition is again attained. Some possible effects of this thermal regime on the survival, growth, and distribution of fish populations in South Bay are then discussed in the light of pertinent literature.

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LOCATION AND MORPHOMETRY OF SOUTH BAY

South Bay extends from Lake Huron into the southeastern end of Manitoulin Island for a distance of 16 miles (Fig. 1). Its major axis inclines northeastward from 45°33′N; 82°00′W to 45°41′N; 81°45′W. The maximum width is 3½ miles but the average is about 2 miles. A narrow passage 70 ft wide connects the bay with Lake Huron and a narrows about ¾ mile wide and located 4 miles from the mouth of the bay divides it into two basins. The total area of South Bay is approximately 33 sq miles and the total volume is 550 × 10^8 ft^3.

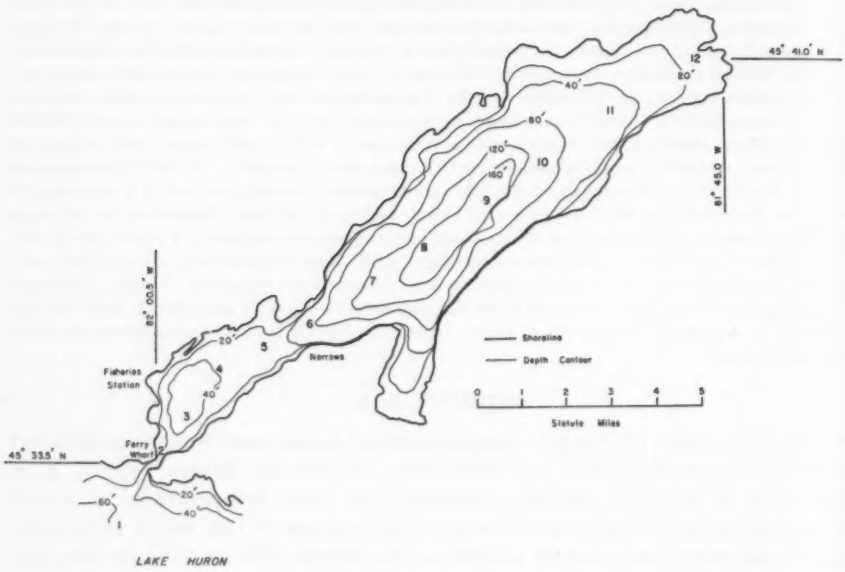

FIG. 1. Bathymetric chart of South Bay, Manitoulin Island, with bathythermograph stations (1–12) indicated.

The outer basin, which comprises 16% of the total area and 7% of the volume of the bay, is a comparatively shallow body with a maximum depth of slightly over 40 ft. About 66% of the volume of this outer basin lies between the surface and the 20-ft contours.

The inner basin deepens rapidly to a maximum depth of 180 ft at station 9, about 5 miles above the narrows (Fig. 1.) Then it shallows rapidly to 80 ft at station 10, some 6 miles above the narrows. The rest of the inner basin, from station 10 to the foot of the bay, is relatively shallow with a gently sloping bottom. About 33% of the volume of the inner basin is less than 20 ft deep and 20% of the volume is from 20 to 40 ft deep.

SOURCES OF TEMPERATURE DATA

The main sources of temperature data used in this report are the series of bathythermograph casts made in South Bay during the decade 1953 to 1962. Each series consisted of a bathythermograph cast made at each of 11 stations along the major axis of the bay and at one station in Lake Huron, 1 mile off the mouth of the bay. The series of casts were made at intervals of 1 or 2 weeks during the months of May to November inclusive, with a few exceptions. A few partial series or individual casts were also made during the months of December through April in some years.

A permanent record was made of each bathythermograph trace by clamping the smoked glass slide bearing the trace into the appropriate viewer grid, inserting the combination into the film holder of a photographic enlarger, and projecting the combined image on sensitized paper. The series of bathythermograph traces are particularly useful in studying the changes in temperature which take place with depth and with location along the bay.

The calibration of the bathythermographs used in these surveys was carried out as follows. As a continuing control, a reading was made with a standard thermometer immersed in a bucket of newly drawn surface water every time a bathythermograph was cast and the average bucket temperature for each weekly series was compared with the average surface temperature reading on the bathythermograph. About once a year, or whenever the instrument was suspected to be drifting out of calibration, the bathythermograph was immersed in a water bath along with a standard thermometer and simultaneous readings were made while the water temperature was varied gradually from 52 to 75 F. Instruments showing any drift were returned to the factory for repair. The bathythermograph data were found to be accurate to about 1 F. Unfortunately, there is no record of calibration before 1958 but, since the instruments were the same as used in following years, it seems unlikely that their accuracy differed significantly.

The other sources of data used here are some daily thermometer readings taken from the ferry wharf at South Baymouth and some thermograph records made at the fisheries station wharf. In general the thermometer readings were made each evening between 7 and 8 PM EST from June 19, 1957 to July 30, 1960 but a rigid time schedule was not adhered to. The thermograph records have been made continuously from midsummer of 1957 to the present, except during a few intervals when the instruments failed to function. The thermometer readings and thermograph records are particularly useful in showing the changes which take place in the temperature over short intervals of time.

Once or twice a year the thermograph reading is compared with the reading on a standard thermometer and an adjustment is made when necessary. The error in the thermograph reading is of the order of ± 1 degree.

GENERAL FEATURES OF TEMPERATURE REGIME

Thermometer Readings at the Ferry Wharf

As Dutton and Bryson (1960) and others have shown, the seasonal cycle of surface water temperature in a lake or similar body can be described approximately by a function of the form $T = T_m \sin 2\pi t/P$, where T is the temperature at any time t, T_m is the amplitude of the annual temperature change, and P is the period of the cycle. The smooth curves from mid March to the middle of the following January in Fig. 2 represent such a function fitted to the daily thermometer readings at South Baymouth ferry wharf. Here the

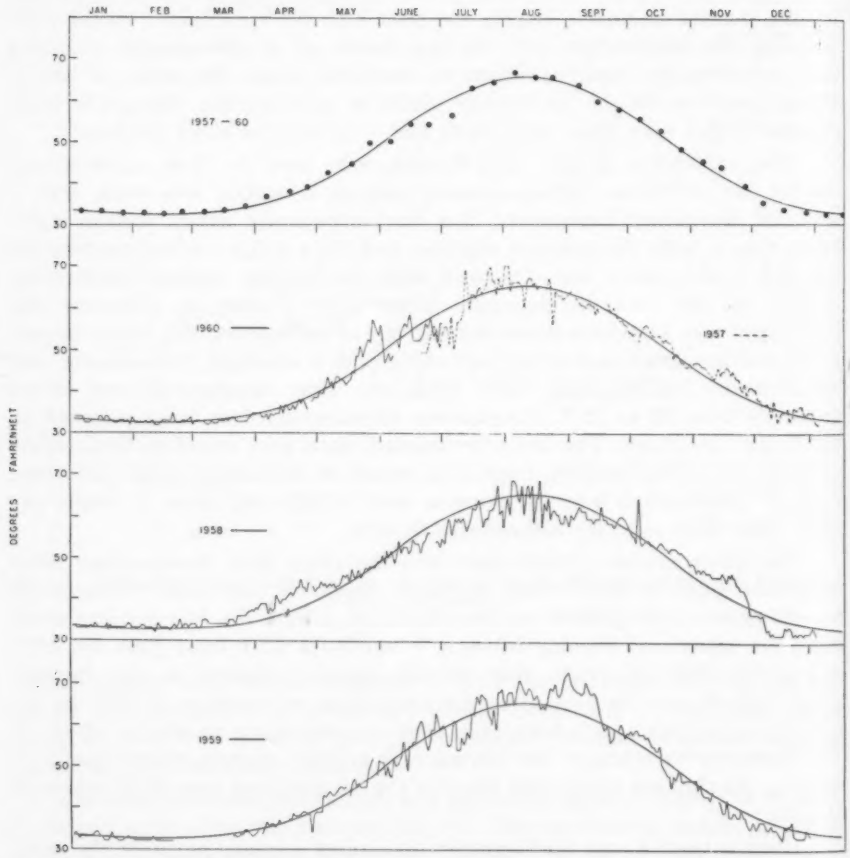

FIG. 2. Surface water temperatures at the ferry wharf, South Baymouth, for the period June 19, 1957 to July 30, 1960. Datum points in the uppermost frame are 10-day means obtained on pooling the data for the 4 years. The smooth curve in each frame represents the function: $T = 16.0 \sin 2\pi t/292$. The irregular lines connect the daily thermometer readings.

temperature ranges from 34 F in the last week of March to 66 F in mid August, from which T_m is 16 degrees. The period is 292 rather than a full year because the sine function obviously does not apply for the period between mid January and mid March, when the temperature remains a constant 33 F to 34 F. During the latter period the bay is usually frozen over and the channel at its mouth may also freeze over from time to time when the weather is exceptionally cold and calm. As a rule, however, waves from Lake Huron tend to keep the channel open.

The seasonal cycle of surface water temperatures at the South Baymouth ferry wharf is at its lowest point from the latter half of January through February and the first half of March. Warming begins about the middle of March, while the bay is still frozen over, and accelerates during April and May. Break up of the ice cover generally occurs around April 19. In the latter part of July and the first 2 weeks of August the warming decelerates until the temperature reaches its peak value about August 12. Thereafter the cooling phase begins. It proceeds at an accelerating rate during the latter half of August and the first half of September and then continues at a steady rate until the last week of November. From that time until the first week of January the cooling decelerates until the temperature again reaches its minimum value about January 10.

The trend of surface water temperatures at the ferry wharf also departs from the sine form during the last week of June and the first week of July, when the observed temperatures are as much as 8 degrees lower than the hypothetical values. The reason for this temperature slump is not definitely known at present but it may be an influx of cold, hypolimnial water from an upwelling in Lake Huron. That such an upwelling does occur off the southeast tip of Manitoulin Island during the period in question has been suggested by Ayers et al. (1956) in their report on the thermal structure of Lake Huron.

Figure 2 also indicates some of the year-to-year variations in the trend of surface water temperatures at the mouth of the bay. For example, during the last 10 days of August and the first 10 days of September 1957 the surface temperatures were about normal, whereas in 1958 they were considerably below average during the same period and in 1959 they were much above average. Or to take another example, the April surface temperatures were as much as 6 degrees above average in 1958, about average in 1959, and slightly below average in 1960. The year-to-year variations in surface water temperatures of South Bay appear to be closely correlated with year-to-year variations in air temperatures (McCombie, 1959).

In addition, Fig. 2 shows a pronounced day-to-day fluctuation in surface water temperature. Some of this fluctuation may, of course, be a sampling error arising from the fact that the thermometer readings were not always made at the same time and hence at the same stage of diurnal warming. However, much of this day-to-day variation in temperature at the ferry wharf may be due to an influx of water from Lake Huron and an efflux from South Bay. During the months of May to October the lake water is cooler than the

epilimnial water of the bay, whereas in the winter months the reverse is true. As can be seen in Fig. 1, the day-to-day variation in the thermometer readings is only 1 or 2 degrees in January, when the difference between bay and lake temperatures is least, but it may be as much as 7 or 8 degrees in July and August, when the difference is greatest. Moreover, observations of the direction of flow of the surface water at the ferry wharf, which were made at the time the thermometer readings were taken, indicated that the flow might be inward one night and outward the next. However, a definite concordance between inflow of cold water and drop in temperature or outflow of warm water and rise in temperature cannot be demonstrated with the present data.

The most detailed study of the exchange of water between South Bay and Lake Huron to date is that made by Bryson and Stearns (1959) during the first week of August 1952. By operating water level recorders at three locations along the bay they were able to detect a seiche having several components with periods ranging from 9.0 to 61.9 min and amplitudes from 0.859 to 2.99 cm. They also estimated that the water mass of the outer basin of South Bay was replaced with Lake Huron water at the rate of 10% per day following a storm.

On July 30, 1962, an experiment was carried out with captive drogues in midchannel at the mouth of the bay. A drogue suspended 3 ft beneath the surface went straight out towards the lake at 0.28 mph while one suspended at 24 ft went straight into the bay at 0.23 mph.

Thermograph Records from the Fisheries Station Wharf

In general the surface water temperatures at the fisheries station wharf follow the same seasonal trend as the surface temperatures at the mouth of the bay, though they are from 1 to 3 degrees higher than the latter during the summer months. This higher temperature at the fisheries station wharf may be due in part to the fact that water is only 5 or 6 ft deep at that location, whereas at the ferry wharf it is 30 to 40 ft deep. It may also be due to the fact that the fisheries wharf is some distance removed from the cold mass of Lake Huron (Fig. 1), for, as will be seen on comparing the bathythermograph data for the several stations along the bay, there is a gradual increase in temperature from the mouth of the bay to the foot.

Besides the seasonal and day-to-day changes in surface water temperatures cited above, the thermograph records from the fisheries station wharf show a pronounced diurnal rise and fall (Fig. 3). Generally the temperature reaches its peak in midafternoon, around 2 PM EST. This peak is of course, associated with the rising of the sun to its zenith with the attendant increase in intensity and penetration of solar energy. A second peak, which sometimes occurs late at night, must be associated with an influx of warm water from the inner basin or with the arrival of a warm air mass over the bay.

There is also some suggestion in both the thermograph records from the fisheries station wharf and the thermometer readings from the ferry wharf of a longer term oscillation of surface temperatures, in which peaks succeed

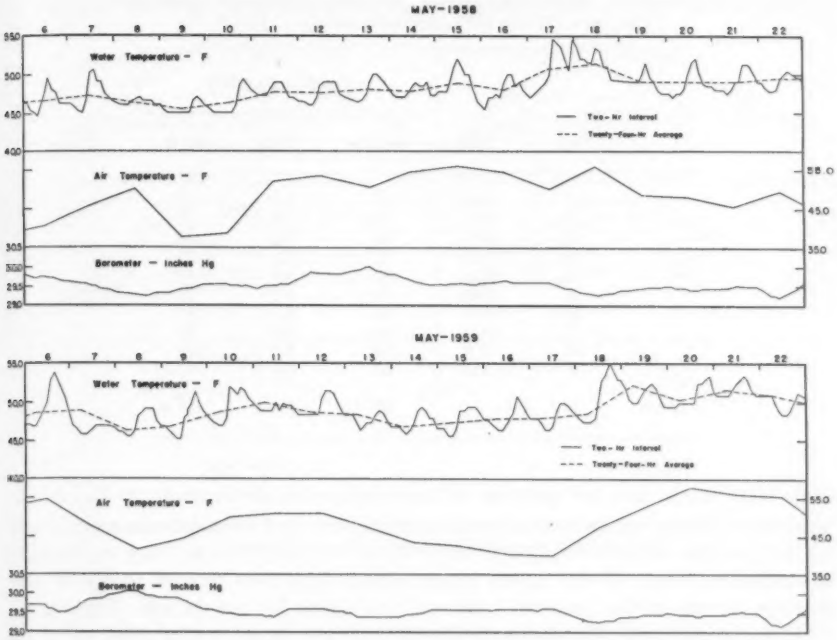

FIG. 3. Surface water temperature, air temperature, and atmospheric pressure at South Bay-mouth for the periods May 6 to 22, 1958 and 1959.

slumps at roughly 3-day intervals (dotted line in Fig. 3). A similar oscillation in surface temperatures has been observed in thermograph records from Lake Opeongo, Algonquin Park, where it did not appear to be related to seiche action or water exchange (R. M. Christie, personal communication). It could be that this component of the water temperature variation is associated with the movement of warm and cool air masses into the area but a clear correlation with air temperatures or atmospheric pressures cannot be demonstrated at present.

BATHYTHERMOGRAPH TRACES FROM OFFSHORE STATIONS

In summarizing the information on the bathythermograph traces it was convenient to read off and tabulate temperatures at an arbitrarily chosen depth interval of 20 ft. These data were first tabulated for the individual years from 1953 to 1962 inclusive and plotted to give a trend line for each depth for each year. Then, when it became evident that these trend lines took the same general form from one year to the next, the data for all years were pooled and mean temperatures were calculated for successive 10-day intervals, as illustrated in Table I. As can be seen, the dates on which temperature observa-

TABLE I. Method for pooling the bathythermograph data for the years 1953 to 1962 (example: station 4, July 1–10).

	Day	Year	Temperature (F) Surface	20 ft	40 ft
	1	1958	57	57	55
	2	1957	59	59	50
	3	1959	61	51	46
	3	1962	67	67	52
	4	1956	60	60	47
	6	1960	55	57	48
	9	1954	61	61	51
	9	1957	62	60	53
	10	1959	60	55	46
	10	1962	65	65	52
Mean	5.7		60.7	59.2	50.0

tions were made and the number of observations made in each 10-day interval varied from year to year. Similar tabulations and calculations were made for each of the bathythermograph stations for the period from May to November inclusive. These 10-day mean temperatures were then plotted to obtain the average picture of the seasonal trend at each depth for the decade (Figs. 4, 5).

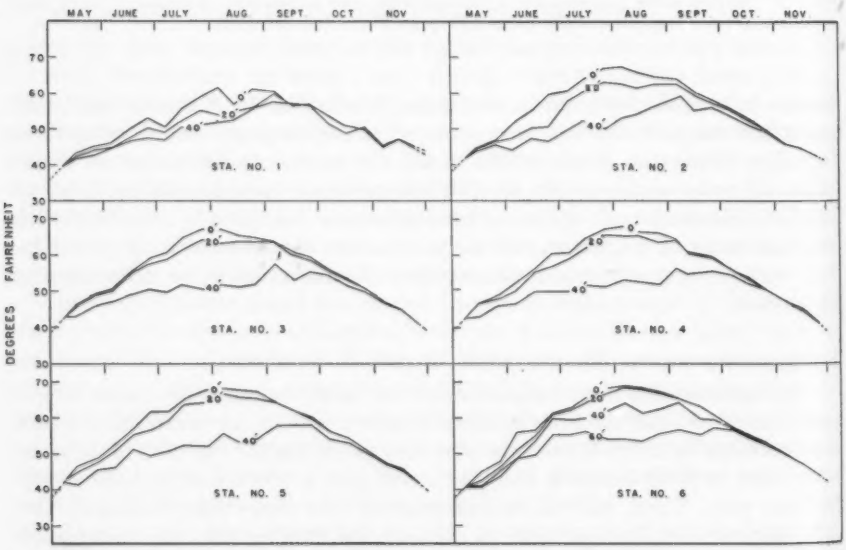

FIG. 4. Seasonal trends of water temperatures at successive 20-ft intervals at stations 1 to 6 based on pooled data for the decade 1953 to 1962.

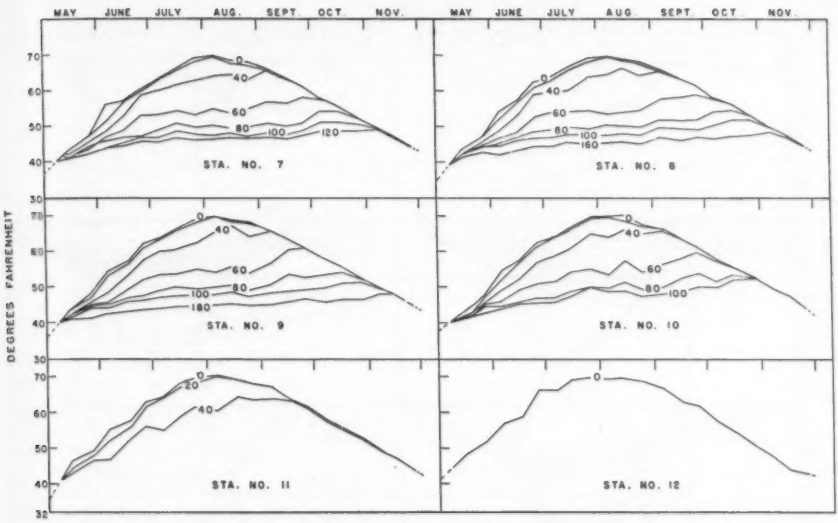

FIG. 5. Seasonal trends of water temperatures mainly at 20-ft depth intervals at stations 7 to 12 based on pooled data for the decade 1953 to 1962.

In turn, data were read off these temperature trends for the 15th day of each month and plotted to give the average vertical temperature section for each month (Figs. 6–9). Temperature data for the months of December through April were not pooled because there were too few traces available for those months to give meaningful averages.

SEASONAL TEMPERATURE TRENDS

In general, the water temperatures at all stations (Figs. 4, 5) approach 40 to 42 F by the first week of May and by the second week thermal stratification has begun. In the first week of June the stratification is well established, as shown by the separation of the seasonal trend lines for successive depths, and a thermocline can be recognized. During the rest of June and July the boundary between the epilimnion and thermocline becomes more and more distinct but the transition from thermocline to hypolimnion remains a gradual one throughout the period of stratification.

With the onset of thermal stratification the surface temperature continues to rise at a rate of about 3 degrees per 10 days until it reaches a maximum value during the first week of August. The maximum attained varies from one station to another, being about 62 F at station 1 in Lake Huron, about 67 F at stations 2 to 6 in the outer basin, and about 70 F at stations 7 to 12 in the inner basin. As pointed out above, the lower temperatures in the outer basin probably reflect the exchange of water between the bay and Lake Huron.

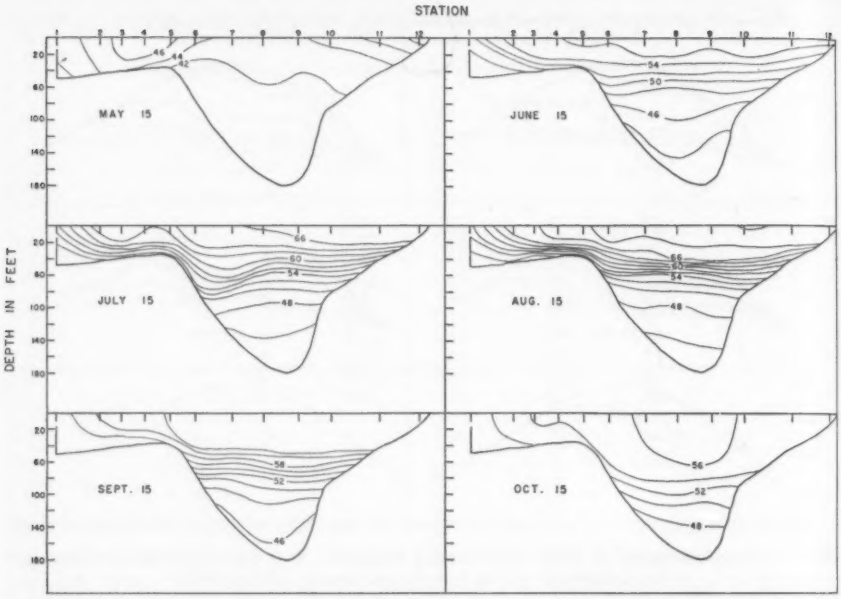

FIG. 6. Mid-monthly vertical temperature sections of South Bay for May to October based on the seasonal temperature trends for the decade 1953 to 1962 shown in Figs. 4, 5. The isotherms are in degrees Fahrenheit.

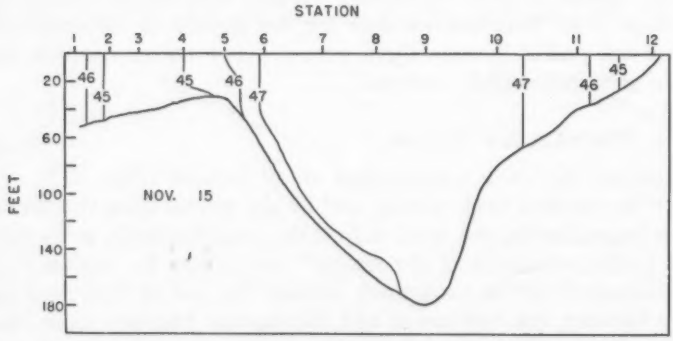

FIG. 7. Mid-monthly vertical temperature section of South Bay for November based on the seasonal temperature trends for the decade 1953 to 1962 shown in Figs, 4, 5. The isotherms are in degrees Fahrenheit.

The temperature at the 20-ft level follows essentially the same trend as the surface temperature, except at the two outermost stations in the outer basin and the lake station. Indeed, at station 6 in the narrows and at stations 7 to 12 in the inner basin the top 20 ft of water is essentially vertically isothermal. Since station 12 is less than 20 ft deep, only the surface temperatures

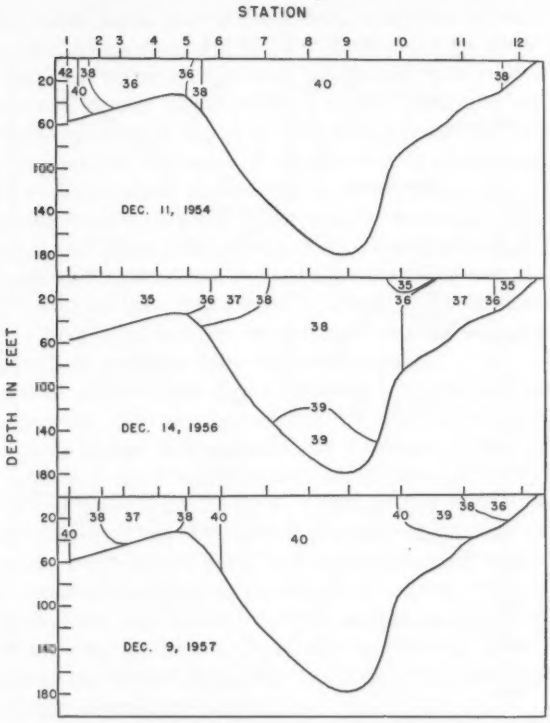

FIG. 8. Early winter vertical temperature sections of South Bay based directly on the few bathythermograph traces available for that period. The isotherms are in degrees Fahrenheit.

are shown in the figure. On the other hand, at station 2 at the mouth of the bay the temperature difference between the surface and 20-ft levels may be as much as 10 degrees in late June and at station 3 it may amount to 3 or 4 degrees. As will be seen later in the section on vertical temperature sections, there would appear to be a wedge of cold water thrusting into the bottom of the outer basin.

From the 40-ft level downwards the water warms more slowly than it does in the top 20 ft and it reaches its maximum at progressively later dates. Moreover, the maximum temperatures reached at the deeper levels are progressively lower than that reached in the top 20 ft. For example, at station 9 the temperature at 40 ft rises about 2 degrees per 10 days until it reaches a maximum of 65 F in mid August, whereas at 80 ft it rises 1 degree per 10 days to a maximum of 54 F in mid October. Nevertheless, even at the 180-ft level there is some warming as the seasons advance and the temperature rises from 34 F in February to 47 F in the first week of November.

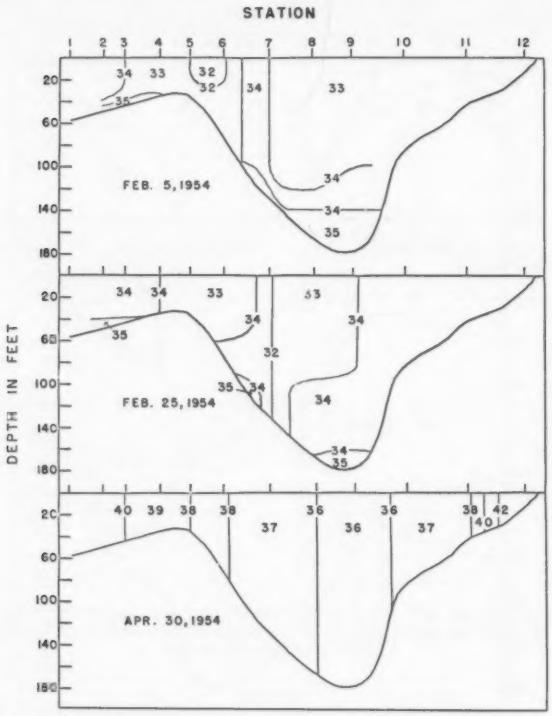

FIG. 9. Late winter and spring vertical temperature sections of South Bay based directly on bathythermograph traces for the period. The isotherms are in degrees Fahrenheit.

In mid November South Bay becomes vertically isothermal at a temperature of about 45 F, as shown by the convergence of the seasonal temperature trends in Figs. 4, 5. The events leading to this isothermal condition follow the familiar coursé described by Ruttner (1953). As the surface layers cool in the late summer and autumn, there is a gradual decrease in the thermal stability of the water mass and heat is stirred into progressively deeper layers as time passes. Consequently the epilimnion becomes deeper and deeper until it eventually absorbs both the thermocline and the hypolimnion. Presumably fall turnover takes place at that time.

VERTICAL TEMPERATURE SECTION

The vertical temperature sections for February 1954 (Fig. 9) indicate that the water mass in South Bay is divided into both columns and layers at the beginning of the year. For example, the section for February 5 shows a column of 34 F water at the mouth of the bay, a column of 33 F water in

the rest of the outer basin and the narrows, a slender column at 34 F just above the narrows, and a wide cell of 33 F water over the deep portion of the inner basin. The 33 F water in the inner basin overlies a layer of 34 F which, in turn overlies still denser water at 35 F. Hence the inner basin is inversely stratified at the beginning of the year. The temperature section for February 25 is similar to that for February 5 except that it shows more 35 F water and less at 33 F. Thus there appears to be some accumulation and possibly a redistribution of heat within the water mass towards the end of the month. Recently Likens and Ragotzkie (1965) have demonstrated that appreciable water movement can take place even when the lakes are ice-covered. The vertical component of this movement is about three orders of magnitude greater than the horizontal and the mechanism involved appears to be convection initiated by heat transfer from the bottom mud.

By the end of April the ice cover has gone from the bay and warming of the water accelerates. The temperatures in the section for April 30, 1954 are from 1 to 9 degrees higher than those in the February 25 temperature section. In the outer basin the April temperatures range from 38 to 40 F, in the deep portion of the inner basin from 36 to 37 F, and at the shallow end of the inner basin from 36 to 42 F. Thus the shallow portions of the bay warm more rapidly than does the deep central core. Rather unexpectedly there is no evidence of horizontal temperature layering in the April section. On the contrary, the water mass is divided into several vertical columns, each having a different temperature but being isothermal from top to bottom. It may be that this condition reflects the vernal turnover in South Bay and that the columns represent vertically circulating water.

During May the thermal stratification begins in South Bay as warmer, lighter surface layers float over the cooler and denser ones below. By the middle of the month (Fig. 6) in the deep central region of the bay a layer of water about 40 ft thick at a temperature of 42 to 44 F overlies water at temperatures between 40 and 42 F. In the outer basin and in the shallow portion of the inner basin the temperatures are higher still, namely 44 to 46 F and 44 to 48 F respectively, and the water from these regions would appear to be closing over the cooler water in the deep, central core. At the same time the water at station 1 in Lake Huron is 3 or 4 degrees cooler than that in the outer basin of the bay and tends to wedge in below the latter.

By the middle of June the warmer waters from the outer basin and the shallows of the inner basin appear to have merged with the surface water over the deep central region to form a continuous layer some 20 to 30 ft deep extending from the mouth of the bay to the foot. Within this layer there is a horizontal gradient with readings ranging from 54 F at the mouth to 56 F at the foot. As pointed out earlier, this gradient is probably due in part to an exchange of water between the bay and Lake Huron. It may also partly due to a more rapid warming of the water at the shallow inner end of the bay.

In the temperature section for June 15 the layer between the surface and the 30-ft level may be regarded as the epilimnion. The thermocline, or

metalimnion, is represented by the zone between the 30- and 60-ft levels, in which the temperature decreases 2 degrees per 10-ft increase in depth (=1.77 C per m). This comparatively steep temperature gradient is indicated by the crowding of the 54 to 48 F isotherms in the section. The remainder of the water mass, which lies between the 60-ft contour and the bottom of the inner basin, constitutes the hypolimnion. However, the transition from thermocline to hypolimnion is never a sharp one in South Bay. Within the hypolimnion the decrease in temperature with increase in depth varies from 2 degrees between the 60- and 80-ft levels to 0.5 degrees between the 160- and 180-ft levels.

By the middle of July the epilimnial temperatures are from 5 to 10 degrees higher than on June 15 and the hypolimnial temperatures about 2 degrees higher. A further crowding of isotherms between the 30- and 40-ft levels indicates a steepening of the thermocline. In addition, the continuity of the 54- to 62-degree isotherms in the July 15 section suggests that the wedge of cold water, which pushes into the bottom of the outer basin from Lake Huron, may even extend into the thermocline of the inner basin. Indeed, the portions of these isotherms which lie within the inner basin are some 20 ft below the portions in the outer basin, giving the impression that cold water from the latter is cascading over the sill at the narrows into the inner basin.

During the first half of August the warming trend continues, the epilimnion of the inner basin deepens to 40 ft and the temperature gradient in the thermocline becomes still deeper. By August 15 the epilimnion is about 2 degrees warmer than it was in mid July and the hypolimnion about 1 degree warmer. The temperature gradient in the thermocline is about 5 or 6 degrees per 10-ft increase in depth in mid August, as compared with 3 degrees per 10-ft increase in mid July. On the other hand, any deepening of the epilimnion of the outer basin which might take place during August and in following months is prevented or obscured by the shallowness of that basin and by the wedge of cold water pushing in from Lake Huron.

In the second half of August the epilimnion begins to cool and in the inner basin it continues to deepen. At the same time the hypolimnion continues to warm slowly.

By September 15 the epilimnion in the inner basin has deepened to 60 ft and is 4 to 5 degrees cooler than it was in mid August. The hypolimnion, on the contrary, is about 1 degree warmer. As would be expected, the cooling of the surface layers is due to a transfer of heat to the deeper layers, as well as to a loss of heat to the atmosphere. Since the resistance of the water mass to mixing is proportional to the difference between densities of the epilimnion and hypolimnion (Schmidt 1928), the downward transfer of heat by turbulent mixing accelerates as the temperatures and densities of these two zones approach the same values.

By the middle of October the epilimnion of the inner basin is from 6 to 8 degrees cooler than it was in mid September and it has deepened to 80 ft. At the same time the temperature gradient in the thermocline has become more gradual, as indicated by the greater spread of isotherms in the October

temperature section. The epilimnial water over the deep central portion of the inner basin is 1 or 2 degrees warmer than that in the narrows or at the shallow inner end.

In mid November the isotherms in South Bay are mainly vertical, indicating that the water mass is vertically isothermal at that time (Fig. 7). However, there is still some horizontal variation in temperature during this month. The water in the outer basin and at the shallow end of the inner basin is still 1 or 2 degrees cooler than that in the deep central portion of the bay. Moreover, by mid November the temperature of the outer basin is about 1 degree lower than that at station 1 in Lake Huron.

In December the temperatures in the outer basin may be from 2 to 6 degrees lower than that at the lake station (Fig. 8). There is also some evidence of an inverse temperature stratification in the inner basin during this month. For example, in the temperature section for December 14, 1956, the 39 F water in the deepest part of the bay is overlain by water at 38 F which, in turn, is overriden in part by 36 to 37 F water from the outer basin. In the section for December 9, 1957, the 40 F water in the central portion of the bay is partly overriden by 36 to 39 F water from the shallow end of the inner basin.

That the shallower parts of the bay are warmer than the deeper in the spring, and cooler during the autumn and winter is perhaps to be expected, if one assumes that the heat exchange across a unit area of water surface is essentially the same at all points on the bay. For each calorie gained or lost through 1 cm^2 of surface the temperature of 1 ml of water will be raised or lowered 1 C. Hence the temperature of a column 1 cm deep would be raised or lowered 1 C whereas that of a column 100 cm deep would be altered by only $\frac{1}{100}$ of a degree. In actuality, of course, this simple situation is likely to be modified by wind stirring.

YEAR-TO-YEAR VARIATIONS IN THE THERMAL REGIME

Having dealt with the general features of the thermal regime of South Bay, as seen in the average water temperatures for the decade 1953 to 1962, we may now consider some of the variations from one year to another. This is done here in terms of the monthly thermal sums above 32 F obtained on planimetering the areas under the seasonal temperature trends (Tables II and III.[3] The data for bathythermograph stations 4 and 9 displayed in these tables are considered to be representative of conditions in the outer and inner basin respectively. Since the data for the 20-ft level are not significantly different from those for the surface except for a slight reduction in the mean monthly degree days, the former have been omitted from the tables. For the same reason the data for the 100-, 140-, and 180-ft levels of the inner basin have been omitted.

[3]To convert data in Tables II and III to monthly mean temperatures use the formula: $\frac{M - d - 32.0t}{t}$. M is the mean thermal sum for each month for the decade, d is the deviation for the particular month and year, and t is the number of days in the month.

TABLE II. Means for the decade 1953 to 1962 of the numbers of degree days above 32 F per month at the surface and at 40 ft at station 4, and the deviations from them for each month for individual years.

	Surface						
	May	June	July	Aug.	Sept.	Oct.	Nov.
Mean[a]	428	712	970	1090	876	656	316
1953[b]	–[c]	–	−80	1	100	60	–
1954	40	16	106	20	10	34	12
1955	46	94	162	100	56	64	–
1956	–	–	−6	−68	−64	−22	82
1957	16	32	22	−38	34	22	34
1958	−16	−51	−20	−92	−36	0	37
1959	–	16	8	96	100	−44	−108
1960	–	−48	−78	2	22	56	–
1961	−44	−108	16	−4	88	60	−10
1962	−18	10	90	−70	−36	12	−56
	40 ft						
Mean	354	506	578	656	720	614	310
1953	–	–	−40	2	−76	88	–
1954	−28	66	6	−82	−78	50	68
1955	−6	−100	5	50	10	80	–
1956	–	–	8	−126	−58	−24	88
1957	−54	112	16	−52	−20	−96	40
1958	30	38	150	0	87	42	34
1959	–	−100	−90	−46	14	−18	−102
1960	–	−114	−38	66	20	−2	–
1961	−8	−16	194	−4	−56	38	−4
1962	56	70	−23	−76	−68	30	−50

[a]Means obtained by planimetering areas under the seasonal temperature trends shown in Figs. 4, 5.
[b]Deviations obtained by planimetering areas under seasonal temperature trends for individual years and subtracting these from the means.
[c]No datum available.

The data in Tables II and III are given to the nearest degree day as calculated from the planimeter readings but they should not be assigned undue precision. Since the bathythermograph readings on which these data are based are only accurate to ±1 degree, deviation of less than 30 degree days must be taken with reservation. Allowance must also be made for variations introduced in calculating the 10-day mean temperatures and interpolating seasonal trend lines between the data for individual years. On the other hand, deviations greater than 30 or 40 degree days are likely significant and the following general observations may be made.

The monthly thermal sums differed considerably from year to year, from month to month, and from one depth to another. There were also differences between stations for any particular year, month, or depth.

TABLE III. Means for the decade 1953 to 1962 of numbers of degree days above 32 F per month at 40-ft intervals at station 9, and the deviations from them for each month in individual years.

	May	June	July	Aug.	Sept.	Oct.	Nov.
			Surface				
Mean[a]	358	744	1076	1116	920	716	410
1953[b]	–[c]	–	−142	−4	30	16	22
1954	8	34	−8	54	0	−4	−28
1955	54	126	124	158	102	116	–
1956	–	–	−42	−26	−78	−36	34
1957	16	16	30	−16	20	−42	−6
1958	22	−70	−60	−16	−32	0	12
1959	–	28	16	80	92	−38	−122
1960	–	−8	−76	14	54	6	–
1961	−22	−120	−62	2	94	92	−20
1962	−16	56	42	−46	−2	−16	−76
			40 ft				
Mean	316	616	898	1012	914	716	410
1953	–	–	−16	14	−26	−16	22
1954	−32	56	−72	−76	−2	−4	−28
1955	58	106	−72	−78	22	66	–
1956	–	–	−78	−46	−82	−48	20
1957	−12	58	60	56	26	42	6
1958	48	−28	4	16	−26	0	12
1959	–	−44	16	28	66	−38	−122
1960	–	−128	−18	44	58	6	–
1961	−2	−20	20	12	100	98	−20
1962	6	44	40	8	−6	−28	−76
			80 ft				
Mean	304	430	542	552	644	644	410
1953	–	–	−56	44	7	24	22
1954	−54	38	−8	4	30	46	−36
1955	28	42	−46	−20	−14	68	–
1956	–	–	−84	−72	−74	−40	−12
1957	−8	32	40	62	52	40	−6
1958	46	108	122	82	164	70	12
1959	–	−36	−76	26	−120	−52	−122
1960	–	−98	−84	−8	−130	−84	–
1961	−10	−12	−14	−24	6	18	−20
1962	−58	−28	−104	−56	−86	−14	−78
			120 ft				
Mean	278	374	438	460	446	516	402
1953	–	–	−84	34	40	44	30
1954	−28	52	44	44	60	134	−34
1955	50	−6	−16	−12	14	−8	–
1956	–	–	−70	−60	−30	−28	−2
1957	10	44	30	36	72	26	2
1958	28	96	132	66	118	140	18
1959	–	−78	−46	−60	−54	−64	116
1960	–	−108	−78	−48	−48	−90	–
1961	4	22	22	2	0	−34	−26
1962	−60	−52	−82	−82	−66	−112	−76

(*Continued*)

TABLE III. Means for the decade 1953 to 1962 of numbers of degree days above 32 F per month at 40-ft intervals at station 9, and the deviations from them for each month in individual years. — (*Concluded*)

	160 ft						
	May	June	July	Aug.	Sept.	Oct.	Nov.
Mean	264	346	400	414	416	456	394
1953	–	–	−74	50	36	32	16
1954	−30	38	14	64	60	68	−34
1955	6	0	2	26	14	24	–
1956	–	–	−52	−48	−25	−42	30
1957	24	40	−4	44	70	62	10
1958	17	62	110	70	120	142	26
1959	–	−40	−22	−48	−62	−58	−108
1960	–	−116	−52	−22	−44	−72	–
1961	12	41	42	24	14	−12	−30
1962	−46	−58	−70	−66	−82	−104	−72

[a]Means obtained by planimetering areas under the seasonal temperature trends shown in Figs. 4, 5.
[b]Deviations obtained by planimetering areas under seasonal temperature trends for individual years and subtracting these from the means.
[c]No datum available.

A close correlation between monthly mean temperatures of the air and surface water at South Bay has been demonstrated in the earlier study (McCombie, 1959) and some evidence of this relation is seen again here. Exceptionally high or low thermal sums for the surface water coincide respectively with exceptionally high or low air temperatures. For example, meteorological records for the decade 1953 to 1962 (Table IV) show that the summer of 1955 was a particularly warm one and this fact is reflected in the water temperatures recorded at South Bay that year. The monthly thermal sums for the surface water were considerably above average throughout the period from May to October inclusive. For the outer basin these sums ranged from 46 degree days above average in May to 162 degree days above in July: for the inner basin, from 54 degree days above in May to 158 degree days above in August.

In contrast, the meteorological and water temperature records for South Bay show that the summer of 1956 was exceptionally cool. The monthly thermal sums for the surface water were below average through July to October inclusive. For the outer basin these sums ranged from 6 degree days below average in July to 68 degree days below in August: for the inner basin, from 26 degree days below in August to 78 degree days below in September. Unfortunately there are no temperature records available for the bathythermograph stations for May and June of 1956.

The summer of 1958 was also cooler than average, as shown by the meteorological and water temperature records. The monthly thermal sums for the surface water ranged from 16 degree days below average in May to 92 degree days below in September: for the inner basin they were from 16 degree days in August to 70 degree days below in June.

TABLE IV. Mean monthly, annual, and seasonal air temperatures in degrees Fahrenheit at South Baymouth, Manitoulin Island, 1953 to 1962.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean	Mean, May to Oct.
1953	20.5	22.1	28.5	38.0	50.3	58.8	64.6	65.9	57.1	49.2	40.1	28.6	43.6	57.7
1954	14.5	25.6	23.1	37.0	46.4	60.2	63.3	64.3	56.1	47.2	38.8	22.8	41.6	56.2
1955	18.2	18.0	24.6	43.8	50.4	61.7	68.5	69.6	54.7	49.5	34.1	19.0	42.7	58.9
1956	15.8	19.2	22.0	35.7	44.2	58.8	61.9	63.0	52.2	49.4	36.9	25.3	38.6	54.9
1957	12.7	20.9	27.4	46.7	47.8	56.9	63.2	61.8	55.7	45.8	37.8	28.0	42.2	55.1
1958	20.3	12.7	31.6	40.0	47.0	54.1	62.5	63.1	57.5	48.6	37.0	15.2	40.8	55.3
1959	13.2	12.1	23.1	37.4	50.0	59.0	64.2	68.0	59.6	45.5	30.6	23.5	40.8	57.8
1960	20.0	18.1	17.7	37.7	51.8	56.5	61.6	63.6	57.7	47.0	39.9	20.0	40.8	56.3
1961	12.2	20.1	27.1	37.9	46.5	55.6	64.5	64.2	61.5	49.3	37.4	25.8	41.8	56.8
1962	14.6	19.9	26.7	37.6	52.2	59.3	63.7	63.4	55.1	48.6	36.9	22.0	40.8	57.0
Mean	16.2	19.1	25.2	39.2	48.7	58.2	63.8	64.7	56.7	48.0	36.9	23.2	41.3	56.6

In August and September of 1959 the cooling of South Bay was delayed markedly by an unusual period of warm, calm weather and the surface water temperatures remained between 65 and 75 F until the end of the second week of September. Hence the thermal sums for the surface water were noteably higher than average for those months. However, these warmer than usual conditions were followed by a more rapid than usual cooling in the next 2 months.

In 1962 the surface water in South Bay was considerably warmer than average during June and July but cooler than average in August and September. In contrast to the situations described in preceding paragraphs, the deviations from the average thermal sums for the surface water found in 1962 do not appear to be related to variations in air temperatures. On the contrary, the monthly mean air temperatures throughout 1962 were close to the average values for the decade.

Variations in Deeper Layers

One might expect that the thermal sums for the thermocline and hypolimnion would deviate from the averages in much the same way as the sums for the surface layers did, because of the exchange of heat between successive layers. Higher than average thermal sums for the surface layer would be accompanied by higher than average sums for the deeper layers and vice versa. And indeed such a relation did hold in the inner basin during the unusually cool summer of 1956, when the thermal sums for the months of July and August were below average at all levels from the surface to 180 ft.

However, in other years the relation between the thermal sums of the surface and deeper layers was an inverse one. For example, in August and September of 1959 the thermal sums for the surface layer in the inner basin were 80 and 92 degree days above average but the sums at depths of 100 ft or more were from 34 to 80 degree days below average.

The inverse relation between temperature conditions in the surface and deeper layers described here is comparable to that reported by Rodgers and Anderson (1963) in their study of the thermal structure of Lake Ontario. They found that: "Surprisingly too, the regime of surface temperatures is not necessarily indicative of heat content [of the entire water mass]; ...In 1959 the peak surface temperature was greater than in 1960, but the peak heat contents were in the reverse order."

We are reminded, therefore, that the variations in temperature conditions shown in Tables II and III were probably due to year-to-year variations in heat transfer as well as to differences in the amount of heat entering the water mass. These variations in heat transfer were likely due in turn to differences in the duration, direction, and velocity of the wind from one year to another. The action of the wind would be twofold, namely: to affect stirring within the bay itself and to increase the exchange of water between the bay and Lake Huron.

DISCUSSION

To conclude this report on the thermal regime of South Bay and set the stage for further investigations it may be worthwhile to consider some of the ways in which the temperature conditions are likely to affect various biological phenomema in that body.

Results of experimental netting and creel censuses indicates that most of the smallmouth bass, *Micropterus dolomieui* Lacépède, taken in South Bay come from the inner basin. Fraser (1955) found that 92% of the bass caught in trapnets set around the shore of the entire bay in 1947 and 1948 came from the northeast half of the inner basin. At the same time he reported that only 11% of the anglers' catch came from the outer basin. More recent creel census records give essentially the same picture. The smallmouth bass is a warm water species having a preferendum of about 70 F (Ferguson, 1958, quoting MS by F. E. J. Fry) and the epilimnion of the inner basin is from 2 to 8 degrees warmer than that of the outer basin throughout June to September inclusive (Fig. 7).

That water temperatures also play an important part in the distribution of the lake trout, *Salvelinus namaycush* (Walbaum), within lakes is well known. Kennedy (1941) investigated the movement of this fish between two adjoining lakes in Algonquin Park, Ontario. He found that White Lake (maximum depth 45 ft) warmed more rapidly than did Big Trout Lake (maximum depth 95 ft) and the lake trout migrated from the former to the latter in the spring. This migration was under way by the first 2 weeks of May when the average temperature of White Lake was 48 F. It reached a peak between May 13 and June 13 when the average temperature was about 63 F and finished between June 28 and July 11 when the temperature reached 70 F.

Martin (1951) has studied the distribution of lake trout in several other Algonquin Parks lakes. For example, in Redrock Lake trout could be taken at all depths from 5 to 50 ft in early June but they were concentrated between the 30- and 50-ft contours, which corresponded to the 50 F and 45 F isotherms respectively. As the surface layers warmed to 57–59 F in late June, the trout moved downward to depths of 15 to 55 ft. The upper limit of distribution at that time seemed to be the 59 F isotherm but again greatest numbers were caught below the 50 F isotherm. Smaller trout were found to have deeper distribution than the larger ones. However, the distribution of trout in Redrock Lake and also in Louisa Lake was influenced by feeding habits as well as by temperatures.

On studying the reproduction of lake trout in Louisa and six other Algonquin Park lakes, Martin (1956) found that they returned to shallow water to spawn in late October, when the surface temperature was from 50 F to 55 F.

Similar correlations between lake trout distribution and water temperatures have also been observed in Lake Simcoe, Ontario (McCrimmon, 1956), in Lac la Ronge, Saskatchewan (Rawson, 1961), and in Cayuga Lake, New York State (Galligan, 1962).

Water temperatures were probably important in the distribution of lake trout in South Bay too, before the lamprey eliminated them from that body. When fisheries investigations were begun there in 1947 there were still native lake trout present, and tagging experiments indicated that these constituted a resident population (Fry, 1952). They could be caught in the outer basin in the spring but migrated into the hypolimnion of the inner basin towards the first week of July. They returned to shallow water to spawn in October but remained within the inner basin. Accounts of the winter fisheries carried out in the bay during the first quarter of the century and results of a few experimental nettings suggest that the lake trout were confined to the inner bay and the narrows during that season. Subsequent plantings of hatchery stock have behaved in much the same way as the native lake trout (Budd and Fry, 1960; Budd, 1957). Experiments with lake trout in a temperature gradient tank indicated that their preferendum is 53.6 F (Ferguson, 1958, quoting MS by R. W. McCauley and J. S. Tait) and the spring migration of these fish into the inner basin of South Bay coincides with the sinking of the 54 F isotherm (Fig. 6) to the bottom of the outer basin and to the thermocline of the inner basin. Conversely, the upward migration in October takes place as the epilimnion of the inner basin cools to 54 F. In winter the lake trout appear to prefer the 40 F water in the deep portion of the inner basin to the 35–38 F water in the outer basin.

It is more difficult to relate the distribution of the lake whitefish, *Coregonus clupeaformis* (Mitchill), in South Bay to water temperatures at present. The preferendum of this species is only slightly higher than that of the lake trout, namely 54.9 F (Ferguson, 1958, quoting MS by F. T. Tomkins and J. M. Fraser) but its behavior differs markedly in certain respects. Tagging experiments have shown that, in contrast to the lake trout which move into the inner basin, whitefish from South Bay migrate into Lake Huron and northern Georgian Bay towards the end of July (Budd, 1957). They return to South Bay by the following spring. However, returns from more recent tagging, which was carried out at the shallow end of the inner basin, suggest that there may be a discrete whitefish population in that basin (unpublished).[4] Sampling with a fine mesh trawl showed that whitefish fry were concentrated toward the foot of the inner basin (D. J. Faber, personal communication) but this may have been related to the location of the spawning grounds rather than to water temperatures.

The pronounced effect of year-to-year variations in water temperatures on the numbers of smallmouth bass in South Bay has been demonstrated by Fry and Watt (1957). They showed that the number of bass in any year-class is correlated directly with the algebraic sum of the monthly deviations from the long term average air temperatures over the months of July through October of the year of hatching. These deviations in air temperatures were in turn directly correlated with the year-to-year differences in surface water

[4]Progress Report, Fisheries Section, Research Branch, Ontario, Department of Lands and Forests, 1964.

temperatures. Warmer than average summers produced stronger than average year-classes whereas cooler summers produced smaller numbers of fish.

On the other hand, the present study may help to explain why attempts to find correlations between the year-class strengths of other species and weather conditions have been less successful. As has been shown here, warmer than average epilimnial temperatures may sometimes be accompanied by cooler hypolimnial temperatures. Consequently, the summer temperature experience of a deep water inhabitant such as the lake trout might be quite unrelated to surface water and air temperatures.

Some investigators have been able to demonstrate a relation between the growth of fish and water temperatures while others have not. Le Cren (1958) found that the annual increment in weight of the European perch, *Perca fluviatilis* Linn., in Lake Windermere was correlated with the number of degree days above 14 C (57 F) for the surface water. Coble (1965) found that the annual length increment of the yellow perch, *Perca flavescens* (Mitchill), in South Bay was correlated with the mean temperature at 20 ft for the period July to September. However, he could find no correlation between the growth of the yellow perch in Lake Erie and temperatures in the work of Eddy and Carlander (1940) and Jobes (1952) or in the data published by Pycha and Smith (1954). Nor could he demonstrate a relation between the growth of smallmouth bass in Lake Opeongo, Algonquin Park, and temperature.

There is also some evidence of the effects of water temperatures on the distribution and life histories of the bottom fauna in South Bay. For example, Cooper (1962) reports that *Pontoporeia affinis* Lindström is found only at depths below 30 ft in the bay and is most abundant at 120 ft. The upper limit of the temperature for this organism is reported to be about 58 F (Ekman, 1915) and at depths less than 30 ft in South Bay the temperature exceeds this during the summer. In addition, Cooper finds that in the shallow outer basin only small young of the year and large, mature, 1-year-old adults are present whereas at 120 ft in the inner basin there are three groups, namely: small young of the year; medium sized, 1-year-old juveniles; and large, mature, 2-year-old adults. This difference between the size and age compositions of shallow- and deepwater populations is similar to that found by Larkin (1948) in Great Bear Lake and may be due to the same cause. Citing Samter and Weltner (1904) to the effect that egg production of *Pontoporeia* is prevented at temperatures above 45 F, Larkin suggests that in deeper waters, where the temperature remains below this value, the reproductive period is prolonged and as a result, "The end of one winter breeding season is brought closer to the beginning of the next so that a 'summer brood' is observed." At the bottom of the outer basin of South Bay the temperature may exceed 45 F by the latter half of June but at 120 ft in the inner basin it does not do so until September or October (Figs. 4, 5.).

It would appear, therefore, that a continuing study of the thermal regime of South Bay could throw considerable light on the behavior of fish and other aquatic populations in that body. Future attempts to relate the survival,

growth, and distribution of such populations to temperature would probably be more productive if more account were taken of the temperatures *in situ* than has been done to date. It is also evident that studies of the role of wind and other weather conditions in the distribution of heat in the water mass would be desirable.

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Effects of Water and Dielectric Thawing Processes on Shelf Life of Double-Frozen Cod and Redfish[1,2]

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ABSTRACT

Analytical taste panel results showed that immersion-thawing in tap water at two different temperatures (7.2 and 15.5 C) and dielectric thawing (at 38 Mc/s) had similar effects on the cold-storage life (at −23 C) of processed, refrozen fillets of cod (*Gadus morhua*) and of redfish (*Sebastes marinus mentella*) (water thawing at 15.5 C only).

Refrozen fillets from Grand Bank cod, captured in March, iced 4 days and frozen, water-thawed, and reprocessed as above, though not quite as good as once-frozen controls, were still of good quality after 35 weeks storage.

Lightly feeding June trap cod, captured in cool (4 C) inshore water, iced, and frozen before and during rigor mortis, then water-thawed and refrozen, were still acceptable after 28 weeks storage, but were considerably poorer than samples frozen once. Quality was similar at both thawing, temperatures (7.2 and 15.5 C) and both conditions of rigor at first freezing.

Heavily feeding July trap cod, captured in warmer (7–9 C) inshore water, similarly handled and similarly processed and refrozen following thawing in water at 15.5 C or dielectrically, were of just acceptable quality up to 32 weeks in storage and were similar to samples frozen once.

Grand Bank redfish, similarly frozen before and during rigor and later processed and refrozen, maintained very acceptable quality up to 28–34 weeks with both thawing procedures and state of rigor at freezing and were equal to samples frozen once. Thiobarbituric acid values increased on storage.

INTRODUCTION

Much research has been carried out by scientists of the Fisheries Research Board of Canada in connection with the commercial development of a frozen fish industry based in part on supplies of fish frozen in the dressed (headed, gutted) condition at sea. Separate studies were concerned with the technical aspects of the thawing procedures, which play an important part in processing refrozen fillets (MacCallum, 1964; MacCallum and Ellis, 1964), and with the quality of the refrozen samples as such (Dyer et al., 1962; MacCallum et al.,

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[2]This is the ninth paper in a series on quality of fish. The tenth and eleventh papers appeared in 1965 (J. Fish. Res. Bd. Canada, **22**: 411–420 and 783–791).

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1964a, 1966). In these earlier studies the effects of different thawing operations on the refrozen, stored samples were not assessed. This aspect, i.e. a study of the relative effect of exposure of the fish to different temperatures and environment created by water, microwave and macrowave (dielectric) thawing methods, is discussed by Peters et al. (1967) and in the present paper. In the former investigation, cod were caught near Sable Island, frozen and later thawed in water at 7.2 C or in a microwave oven (2450 Mc/s), processed, and refrozen. Storage quality of the finished fillets was shown to be independent of the thawing procedure. The present paper describes frozen storage tests on cod (a) thawed in tap water controlled at temperatures of 7.2 and 15.5 C, respectively (b) thawed in water controlled at a temperature of 15.5 C or in a dielectric device (operated at macrowave frequency 38 Mc/s) and on redfish (*Sebastes marinus mentella*) processed, refrozen, and stored after having been thawed in 15.5 C tap water or in the dielectric thawer.

There are numerous reports of successful thawing using the dielectric (Jason and Sanders, 1959, 1962a, 1962b; MacCallum, 1964; Bengtsson, 1964), microwave (Bengtsson, 1964), humidified air (Merritt and Banks, 1964; Karsti, 1964), and water methods. The last was tried on both plate (MacCallum and Ellis, 1964; Merritt and Banks, 1964) and brine frozen fish (Magnusson, 1952; Magnusson and Hartshorne, 1952; Peters and Slavin, 1960).

Dyer et al. (1962) showed that refrozen (after thawing in tap water at about 8 C) fillets of trap-caught cod captured in a particular period of the summer fishery (third week in July 1961) developed poorer texture in storage at −23 C or at −18 C than gutted, unfilleted cod subjected to a single freezing and likewise stored. A similar trend was noted in thawed (in tap water at 15 C) and refrozen fillets of trap fish captured in cool (4 C) inshore water on June 27, during the 1962 catching season (MacCallum et al., 1966). The latter investigation also showed that trap fish, captured in warmer (7 and 11 C) waters while feeding heavily on July 19 and 30, iced, filleted during rigor, and frozen once, were of only fair texture (63–70, respectively) immediately thereafter in contrast to samples prepared from lightly feeding fish captured earlier in the season (June 27). The June samples still graded high (over 70) after storage at −23 C for 6 months. It was of interest especially to determine whether cod from the 1962 trap catches would deteriorate more rapidly on storage after thawing at 15 C than at 7 C.

EXPERIMENTAL

Thawing in Tap Water at 7.2 and 15.5 C

Grand Bank cod (fig. 1)

Market size (6 lb gutted weight) cod, netted in an otter trawl on the southwest edge of the Grand Bank on March 24, 1962, gutted and iced at sea and frozen after rigor mortis, were later thawed after two different periods of storage as dressed fish, processed, refrozen, and stored using procedures described previously (MacCallum et al., 1966).

STARTING MATERIAL	PREPARATION, FREEZING (AFTER RIGOR MORTIS), AND STORAGE (at –23 C)
Gutted Grand Bank cod iced for 4 days on the research vessel *A. T. Cameron*	I. Once-frozen (1¼ hr) finished fillets (controls) II. Once-frozen (5½ hr) 40-lb, 8 × 36 × 4½-inch (thick) blocks of dressed fish (controls) III. Similar to II above, thereafter used to produce refrozen (1¼ hr) finished fillets after: (a) thawing in water at 7.2 C (4¾ hr) (i) 7 days after capture (ii) 8 weeks after capture (b) thawing in water at 15.5 C (3¼ hr) (i) 7 days after capture (ii) 8 weeks after capture

FIG. 1. Flow diagram showing treatment of March 24, 1962, Grand Bank catch of cod.

TRAP COD (FIG. 2)

Fish of 2–3 lb gutted weight, captured near St. John's on June 27, 1962, in cool (4 C) surface water, gutted and iced at the trap and frozen before and during rigor, were later thawed after two different periods of storage as dressed fish, processed, refrozen, and stored using the procedures described previously.

THAWING IN TAP WATER AT 15.5 C AND AT MACROWAVE (38 MC/S) ELECTRICAL FREQUENCY

TRAP COD

Cod of 3 lb gutted weight were captured in 7 C water at St. John's on July 19, 1962. They were gutted, iced at the trap, headed, frozen before rigor, and stored; 12 weeks later the dressed fish were thawed dielectrically and in water (as described previously), processed, refrozen, and stored. Blocks for dielectric thawing[3] weighed approximately 100 lb and those for water thawing 25 lb. Both were of the same length (36 inches) and thickness (4½ inches). Those used for water thawing measured about 5 inches in width, for dielectric thawing about 20 inches. Each thawing operation lasted 1½ hr. Dielectric thawing was carried out in the Radyne thawer[4] as described by MacCallum (1964).

Other cod of 3 lb gutted weight were captured in 9 C water at Catalina, Trinity Bay, on July 25, 1962. After 24 hr storage in ice the fish, then in rigor,

[3]Courtesy Fishery Products Limited, Catalina, Trinity Bay, Nfld.
[4]Product of Radyne Limited, Wokingham, Berkshire, U.K.

STARTING MATERIAL		PREPARATION, FREEZING (AFTER RIGOR MORTIS), AND STORAGE (at −23 C)
Gutted, iced trap cod	Freezing before rigor mortis	I. Once-frozen (1¼ hr) finished fillets (controls)
		II. Once-frozen (5½ hr) 25-lb, 5 × 36 × 4½-inch (thick) blocks of dressed fish (controls)
		III. Similar to II above, thereafter used to produce refrozen (1¼ hr) finished fillets after:
		(a) thawing in water at 7.2 C (3 hr) (i) 1 day after capture (ii) 12 weeks after capture
		(b) thawing in water at 15.5 C (1½ hr) (i) 1 day after capture (ii) 12 weeks after capture
	Freezing during rigor mortis	IV. Similar to I above
		V. Similar to III above

FIG. 2. Flow diagram showing treatment of June 27, 1962, trap-caught cod.

were frozen and, 12 weeks after capture, were thawed, processed, and refrozen following the same procedure described immediately above, with the exception that the water thawing operation lasted 3½ hr. The time required for thawing was determined by the dimensions (14 × 42 × 4 inches) of the 80-lb blocks. Again, the operation in the dielectric thawer was of 1½ hr duration.

REDFISH (FIG. 3)

Fish of about 1¼ lb dressed weight, trawled on the eastern edge of the Grand Bank on October 2, 1964, and headed, gutted, and iced immediately, were frozen before or during (24 hr following capture) rigor mortis as packaged, skinned fillets or, without further treatment, were frozen in blocks. After two different periods of storage, the latter were water-thawed (as described earlier for cod) or dielectrically thawed, processed, refrozen, and stored.

Unlike the case for cod (MacCallum, 1964), the treatment given redfish in thawing in the Radyne dielectric thawer has not been described previously. In the first operation (3 weeks after capture) the blocks of redfish, immersed in water, were carried in plastic trays through the thawer at a belt speed of 7 inches/min. Five of the six generators were in operation, two producing half power, three full power. In the second operation (9 weeks after capture) six generators were used and the conveyor speed increased from the previous

STARTING MATERIAL		PREPARATION, FREEZING (AFTER RIGOR MORTIS), AND STORAGE (at −23 C)
Dressed and iced redfish	Pre-rigor freezing	I. Once-frozen (2½ hr) finished[a] fillets packed in 12-oz cartons, sealed in Saran
		II. Once-frozen (10 hr) 80-lb, 14 × 42 × 4½-inch (thick) blocks of dressed fish were used to produce refrozen (1 hr) finished[a] fillets (packed in 12-oz cartons, sealed in Saran) after:
		(a) thawing in water at 15.5 C (3½ hr) (i) 3 weeks after capture (ii) 9 weeks after capture
		(b) thawing (1½ hr) in the Radyne dielectric thawer (i) 3 weeks after capture (ii) 9 weeks after capture
	In-rigor freezing	III. Similar to I above
		IV. Similar to II above

[a]Skinned and trimmed in contrast to most commercial packs of scaled, skins-on fillets.

FIG. 3. Flow diagram showing treatment of October 2, 1964, redfish.

setting. Difficulties were encountered in the operation of some of the generators, with the result that all power was turned off and the belt stopped on several occasions. The fish were actually in the thawer about 2 hr and exposed to the effect of the energized plates for about 1½ hr. Following thawing on these two occasions the fish had reached quite a wide range of temperatures. Only those with a surface temperature of 14.3 C or lower were immediately iced and used in the frozen storage experiments.

Observations were made of temperatures encountered while thawing redfish in the dielectric thawer and on the condition of the fish for filleting and refreezing.

METHODS OF ASSESSMENT

Taste panels, based on procedures referred to previously (MacCallum et al., 1966), were conducted on all once-frozen controls and twice-frozen samples of cod and redfish. As in the case of cod, redfish were baked according to the procedure of Dyer and Dyer (1949) modified for frozen fish (Dyer et al., 1964a). A scale of 0–100 was used for scoring, based on scores of 80–90 for fish of high quality. Those below 40 were unacceptable. While panelists were trained to

record changes in both taste and texture, in stored redfish it was considered essential to emphasize taste characteristics in calculating overall rating scores. This was done in the same manner that texture characteristics were emphasized in determining overall rating scores for cod.

In addition to taste panel tests, total lipid (Bligh and Dyer, 1959), free fatty acids, and salt extractable protein (Dyer et al., 1950, 1964b), and thaw drip (Dyer et al., 1962) determinations were carried out on the frozen samples of July-caught trap cod and the redfish. The thiobarbituric acid test (Tarladgis et al., 1960), peroxide (Dyer and Morton, 1956), and *p*H (direct and homogenate in iodoacetate (Marsh, 1952, modified such that the weight of fish to buffer is 1:2) methods) determinations were also done on the redfish.

Snedecor's (1961) system was followed for statistical analyses of the data, using the selected procedures referred to earlier (MacCallum et al., 1966).

RESULTS AND DISCUSSION

Thawing in Water at 7.2 and 15.5 C

Grand Bank cod (table I)

For fish frozen once, quality was either fairly constant (dressed samples) during storage or dropped (fillets) but samples of the two treatments did not differ statistically. At 25 weeks the fillets still scored 74, equal to the highest score given freshly frozen fillets of offshore cod examined between August and December 1961 (Dyer et al., 1962).

For fillets refrozen 3 days after the first freezing, quality was lower ($P < 0.05$) than for the controls frozen once only at 17 weeks (samples thawed at 15.5 C) and at 35 weeks (both samples).

For fillets refrozen 7 weeks after the first freezing and prepared from material thawed at 7.2 C, quality at 9 and 13 weeks was poorer ($P < 0.05$) than that of the control fillets. At 11 weeks refrozen samples from material thawed at both temperatures were poorer than the fillet control; at 17 weeks both refrozen samples were poorer ($P < 0.01$) than the dressed control; but at 25 weeks neither of the refrozen samples differed from either control.

In the material refrozen after 3 days, fish thawed at 7.2 C had higher quality than that thawed at 15.5 C after storage for 17 weeks ($P < 0.05$) and for 35 weeks ($P < 0.01$). In the material refrozen after 7 weeks, fish thawed at 15.5 C were not significantly higher in quality than that thawed at 7.2 C. Thus, temperatures of the thawing water within the range 7.2–15.5 C can have varying (but on the average about equal) effects on the refrozen storage quality of cod which would have possessed good qualities if frozen only once and stored.

Trap cod taken in June (fig. 4)

For all samples frozen once, quality was high initially. While it depreciated in frozen storage the rate was not rapid and about equal for the differently prepared samples.

TABLE I. Average taste panel scores,[a] during storage at - 23 C, for dressed and filleted cod from fish captured on the Grand Bank on March 24, 1962, landed in ice after the resolution of rigor and stored after single and double freezing.

(A)		Controls, frozen once					
		Dressed fish			Fillets		
Storage, to the nearest week							
Total	Refrozen	Texture	Taste	Overall rating	Texture	Taste	Overall rating
1		94±2.6	91±2.8	91±2.9 (15)	87±2.0	84±2.6	86±1.7 (62)
3		–	–	–	85±2.4	81±2.6	84±3.3 (17)
5		75±5.1	71±5.9	74±5.0 (17)	80±3.8	80±5.0	77±3.4 (17)
9		68±4.5	67±7.3	69±4.7 (18)	82±5.3	84±3.9	81±5.4 (17)
11		–	–	–	87±3.1	82±5.2	85±2.8 (20)
13		81±3.6	72±5.6	78±3.6 (18)	83±4.5	80±4.8	80±2.6 (17)
17		84±3.5	79±3.4	84±2.6 (16)	77±4.3	68±4.1	76±3.3 (17)
25		78±4.4	74±5.8	78±4.4 (15)	74±5.0	71±4.9	74±4.7 (15)
35		80±4.0	79±3.5	80±2.8 (24)	–	–	–
(B)		Fillets, prepared from frozen dressed fish held 3 days, processed and refrozen after thawing in water					
		At 7.2 C			At 15.5 C		
1		88±3.3	81±4.4	86±2.9 (17)	86±2.9	82±3.9	85±2.5 (17)
3		79±3.6	72±4.3	76±3.0 (17)	77±5.8	77±3.1	77±4.5 (17)
5		77±4.5	81±3.1	78±4.2 (17)	75±5.3	81±5.9	78±4.5 (17)
9		84±2.9	81±1.3	82±2.2 (18)	79±8.0	72±4.6	76±4.0 (18)
17		73±2.3	66±5.9	72±4.2 (16)	61±4.6	66±2.3	64±3.8 (16)
35		70±3.7	70±2.0	70±3.7 (24)	48±3.3	40±4.4	44±2.0 (24)
(C)		Fillets, prepared from frozen dressed fish held 7 weeks 3 days, processed and refrozen after thawing in water					
		At 7.2 C			At 15.5 C		
9	2	65±3.8	73±3.2	67±3.4 (22)	70±6.4	77±3.4	74±3.7 (22)
11	4	74±4.3	76±3.7	74±3.9 (20)	70±4.8	79±3.9	72±4.2 (20)
13	6	67±5.4	70±3.3	68±4.5 (18)	77±4.9	74±3.7	77±4.1 (17)
17	10	63±4.9	76±4.5	71±1.7 (16)	60±6.0	76±4.4	67±4.5 (17)
25	18	65±6.8	65±5.9	65±6.5 (15)	71±6.9	70±5.7	72±5.8 (15)

[a]Average scores are followed by the standard error of the mean. The numbers of judgments (in parentheses) shown with the overall rating scores are common to taste and texture scores.

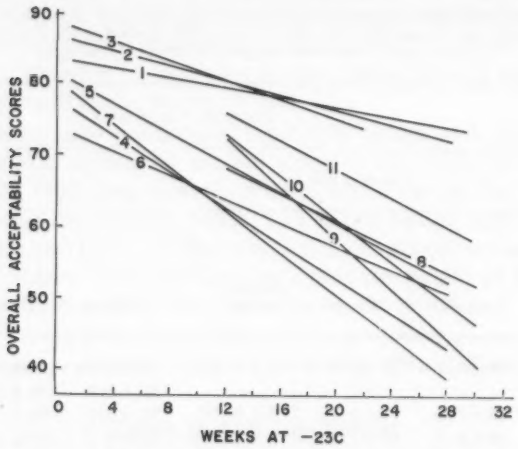

FIG. 4. Regressions of taste panel overall ratings on the total times in storage at −23 C of once- and twice-frozen trap cod caught June 27, 1962. *Samples 1-3*, controls: once-frozen before rigor as (1) dressed fish and (2) finished fillets, and in rigor as (3) finished fillets; *samples 4–7*, fillets refrozen from blocks of dressed fish after 1 day's storage: (4) before rigor and (5) in rigor at first freezing, thawed in tap water at 7.2 C, processed, refrozen, and stored; (6) before rigor and (7) in rigor at first freezing, and thawed at 15.5 C; *samples 8–11*, fillets refrozen from dressed fish after 12 weeks' storage: (8) before rigor and (9) in rigor at first freezing, and thawed at 7.2 C; (10) before rigor and (11) in rigor at first freezing, and thawed at 15.5 C.

For fish frozen twice, quality dropped following the thawing and refreezing processes at a considerably faster rate in most instances than that experienced in the samples frozen only once. The twice-frozen samples reached a level of 40–55 (just above the acceptable grade) 28 weeks after capture.

In the samples thawed and refrozen after 1 day storage and after 12 weeks, there was no correlation of quality of refrozen cod with the temperature of the water used in the thawing operation; for material of the first series initially frozen before rigor mortis those samples thawed at 15.5 C were preferred and for material initially frozen during rigor the samples thawed at 7. 2 C were best; for samples of the second series initially frozen before rigor, scores were practically the same independent of temperature of thawing, while samples initially frozen during rigor and later exposed to a temperature of 15.5 C were preferred.

In comparing these results with those described in the previous section it is apparent that a rise in temperature (occasioned by thawing in water at *either* 7.2 or 15.5 C) followed by refreezing and storage resulted in lower cold storage quality. There was more rapid deterioration in the texture and taste characteristics in twice-frozen trap fish of high initial quality than in Grand Bank cod of equally high quality. Yet, in the following paragraphs, it will be

shown that the higher thawing temperature (15.5 C), when applied to heavily feeding trap fish captured in warmer water during the latter part of July, resulted in only minor loss in the quality characteristics of a relatively poor, once-frozen pack.

Thawing in Tap Water at 15.5 C and at Macrowave (33 Mc/s) Electrical Frequency

TRAP COD TAKEN IN LATE JULY

Taste panel assessment (*Table II*). For fish frozen once and for others refrozen later, initial scores for July 19 and 25 samples were much lower than those for the June 27 samples described above. The low initial quality is in line with that reported previously for July landings of trap fish (Dyer et al., 1962; MacCallum et al., 1964b; 1966).

On the average, thawing and refreezing coupled with additional cold storage did not alter quality greatly. The water-thawed and dielectrically thawed samples were given practically identical ratings.

Other assessment (*Tables III and IV*). Thaw drip values for the control fillets frozen before rigor averaged 6.5% during storage for 24 weeks, similar to those recorded for fish taken on trawl lines in Trinity Bay on October 23 (MacCallum et al., 1964a), and for other trap fish caught during the fourth week in July at St. John's (Dyer et al., 1962). However, refrozen fillets produced considerably more drip, averaging 15.2 and 19.1% — not significantly different one from the other — for the dielectrically and water-thawed samples, respectively. Like amounts of drip were reported for twice-frozen cod taken on trawl lines on October 23 and in traps on July 25 in Trinity Bay (MacCallum et al., 1964a). For twice-frozen samples originally frozen during rigor, average values (15.1% for water-thawed and 15.6% for dielectrically thawed) did not differ significantly one from the other nor from the average value (12.5%) for the fillets frozen once.

Thawing and refreezing did not alter values for total lipids (TL), which were high by other standards (Dyer and Fraser, 1959; MacCallum et al., 1964a), but did result in slightly increased free fatty acid (FFA) production from that of samples frozen once. Initial values for FFA are high with respect to cod from other fisheries but typical of other trap landings (MacCallum et al., 1964a). The values were not significantly lower for the samples thawed dielectrically than for those thawed in water.

Protein extractability in 0.6 M salt solution (EPN values) showed little decrease in once-frozen samples at 32 weeks storage from that expected (Dyer and Dingle, 1961) for freshly frozen cod. However, EPN values for twice-frozen fillets thawed by both methods were low. The value for the water-thawed samples (0.99% wet weight) showed greatly reduced extractable soluble protein.

REDFISH

Observations on the thawing process. In the first thawing operation the temperature of the water in the tray and that of the top surface of the pre-rigor

TABLE II. Average taste panel scores[a] during storage at–23 C for dressed and filleted trap cod captured in July 1962 in two areas, landed ini ce and stored after single and double freezing.

Weeks in storage		Controls, frozen once						Fillets, prepared from frozen dressed fish held 12 weeks, processed and refrozen after thawing					
		Dressed fish			Fillets			In water at 15.5 C			In macrowaves (38 Mc/s)		
Total	Refrozen	Texture	Taste	Overall rating	Texture	Taste	Overall rating	Texture	Taste	Overall rating	Texture	Taste	Overall rating
Prepared before onset of rigor in trap cod caught at St. John's on July 19													
12	0	70±2.8	68±3.6	67±4.0 (21)	73±5.1	55±4.1	66±3.8 (21)	46±4.3	51±4.5	48±4.1 (21)	50±5.2	51±3.5	47±4.3 (21)
17	5	52±3.7	58±2.8	54±3.5 (24)	57±5.8	56±3.5	57±5.5 (24)	46±4.0	51±4.0	48±4.0 (24)	53±5.4	58±2.8	55±4.1 (24)
24	12	56±5.0	67±3.1	63±3.3 (24)	–	–	–	35±4.0	46±5.2	41±2.8 (24)	44±4.3	59±3.8	50±3.3 (24)
32	20	46±4.3	58±3.5	50±2.0 (24)	62±5.2	57±4.0	63±3.9 (24)	35±4.4	46±4.9	40±4.1 (24)	43±4.6	44±3.8	42±3.4 (24)
Prepared from in-rigor cod caught at Catalina, Trinity Bay, on July 25													
12	0	53±4.4	66±4.5	58±3.8 (21)	52±4.6	56±3.6	52±4.0 (21)	48±4.5	54±3.6	50±4.3 (21)	49±5.0	53±4.5	50±4.2 (21)
17	5	40±3.9	52±5.2	44±4.2 (24)	62±4.3	67±1.9	64±2.9 (24)	53±4.7	56±3.7	54±3.7 (24)	48±5.3	58±3.7	53±3.8 (24)
24	12	–	–	–	–	–	–	45±4.6	52±4.5	47±3.0 (24)	53±4.5	55±2.1	53±4.5 (24)
32	20	35±3.9	48±4.6	40±4.2 (24)	60±5.0	62±4.0	58±6.1 (24)	43±5.2	52±4.8	44±4.7 (24)	45±4.6	48±3.8	47±4.0 (24)

[a]Average scores are followed by the standard error of the mean. The numbers of judgments (in parentheses) shown with the overall rating scores are common to taste and texture scores.

TABLE III. Chemical assessment, during storage at −23 C, of dressed and filleted trap cod caught at St. John's on July 19, 1962, landed in ice before the onset of rigor and stored after single and double freezing.

Sample[a]	Weeks in storage: Total	Weeks in storage: Refrozen	Thaw drip (% wet wt.)	Total lipid (% wet wt.)	Free fatty acids (% TL)	EPN[b] (% wet wt.)
(1)	12		4.5	0.72	22.2	–
(2)			4.6	0.87	22.1	–
(3)		0	17.9	0.99	21.9	–
(4)			13.0	0.98	18.8	–
(1)	17		18.9	0.79	28.3	–
(2)			7.0	0.87	14.0	–
(3)		5	19.0	0.93	29.2	–
(4)			17.3	0.89	24.6	–
(1)	24		10.8	0.97	18.9	–
(2)			7.9	1.04	18.4	–
(3)		12	20.5	0.99	28.4	–
(4)			15.2	1.00	23.7	–
(1)	32		–	1.03	20.5	1.90
(2)			–	0.96	20.7	2.04
(3)		20	–	0.97	23.6	0.99
(4)			–	0.90	23.7	1.64

[a] Samples 1 and 2, controls frozen once: (1) dressed fish, (2) fillets; samples 3 and 4, refrozen fillets: prepared from frozen dressed fish held 12 weeks, processed and refrozen after thawing (3) in water at 15.5 C, (4) in macrowaves (38 Mc/s).

[b] Protein extractability in 0.6 M salt solution.

fish was about 21 C as the fish were conveyed out of the thawer, about 1½ hr after entering. The bottoms of the blocks were warmed to about 19 C and the centres to about 7 C. Temperatures in the fish frozen during rigor were about the same, 27 C at the corners of the block, 20 C on the top surface, −.06 C at the centre. In the second thawing operation the fish in the two blocks were warmed to 27–35 C on the surface, 18 C at the centre.

Thus, in the dielectric thawer the redfish did not thaw as uniformly as might be desired. During the first thawing run some of the fish were too hard to fillet soon after leaving the thawer. In contrast, the fish thawed in water could be filleted more readily. All the fish thawed in water could be used since none were overheated; the fish lost little of the pigmentation characteristic of the live animal (perhaps an important point in the production of skins-on refrozen fillets). The surface fish in the dielectrically thawed blocks were bleached, but even they possessed a much fresher appearance than that of iced redfish commonly landed from trawlers.

TABLE IV. Chemical assessment, during storage at −23 C, of dressed and filleted trap cod caught at Catalina, Trinity Bay, on July 25, 1962, landed in ice during rigor and stored after single and double freezing.

Sample[a]	Weeks in storage: Total	Weeks in storage: Refrozen	Thaw drip (% wet wt.)	Total lipid (% wet wt.)	Free fatty acids (% TL)	EPN[b] (% wet wt.)
(1)	12		3.7	0.90	13.3	–
(2)	↓		7.7	0.92	15.9	–
(3)	↓	0	15.1	0.83	19.9	–
(4)	↓	↓	11.9	0.90	16.3	–
(1)	17		14.4	1.02	14.6	–
(2)	↓		14.4	0.95	15.4	–
(3)	↓	5	12.7	0.95	29.3	–
(4)	↓	↓	17.5	0.86	21.6	–
(1)	24		5.8	0.90	18.6	–
(2)	↓		15.4	0.92	19.9	–
(3)	↓	12	17.4	0.97	23.6	–
(4)	↓	↓	17.5	0.93	19.3	–
(1)	32		–	0.81	20.0	2.20
(2)	↓		–	0.95	19.0	2.09
(3)	↓	20	–	0.85	29.5	1.47
(4)	↓	↓	–	1.02	26.0	1.34

[a]Controls, frozen once (1) dressed fish, (2) fillets. Fillets prepared from frozen dressed fish held 12 weeks, processed and refrozen after thawing (3) in water at 15.5 C, (4) in macrowaves (38 Mc/s).

[b]Protein exactibility in 0.6 M NaCl solution.

Taste panel assessment (*Table V*). For fish examined here the method of weighting (mentioned earlier) yielded overall rating scores about equal to the separate texture and taste assessments (in agreement with the experience of Dyer et al., 1956).

The shelf life (to unpalatability) of 72 weeks for once frozen fillets of iced redfish, reported by Dyer et al., (1956), was easily attained. In the present work initial grades were somewhat lower than those given the Dyer et al. samples. Thus, it would appear that the present frozen-at-sea samples may have deteriorated slightly more slowly in frozen storage than those studied by the earlier workers. More important still to the success of freezing-at-sea practices, the texture and taste of the samples originally frozen before and in rigor mortis and subsequently thawed, refrozen, and stored were at all times equal to those of the once-frozen samples. Twice-frozen samples from the two conditions of rigor were of similar quality, as were samples prepared from fish in the same stages of rigor but thawed by the two methods.

TABLE V. Average taste panel scores,[a] during storage at −23 C, for fillets of redfish trawled on October 2, 1964 on the Grand Bank, boated, iced before and during rigor mortis, and stored after single and double freezing.

Weeks in storage		Controls, frozen once					
		Pre-rigor			In-rigor		
Total	Refrozen	Texture	Taste	Overall rating	Texture	Taste	Overall rating
4		69±3.0	72±3.3	72±3.3 (22)	83±2.4	87±3.1	87±2.9 (23)
10		74±1.4	72±2.7	73±2.8 (24)	79±3.4	73±3.0	74±2.7 (24)
16		70±1.9	76±1.9	76±1.9 (23)	80±1.6	75±2.0	76±1.7 (25)
22		74±2.0	69±2.5	69±2.5 (22)	72±1.9	65±2.5	66±2.2 (21)
28		73±1.9	72±2.1	72±2.1 (22)	67±1.9	70±2.0	70±2.0 (21)
34		54±2.2	56±2.6	56±2.6 (21)	62±1.9	58±2.7	58±2.5 (17)
59		62±2.7	58±3.2	59±2.8 (23)	58±1.8	52±2.8	54±2.4 (24)
88		52±1.5	48±2.5	48±2.4 (32)	52±2.0	41±2.5	43±2.1 (31)

Refrozen fillets, prepared from pre- and in-rigor frozen dressed fish held 3 weeks, processed and refrozen after thawing

		Water at 15.5 C						Macrowaves (38 Mc/s)					
		Pre-rigor			In-rigor			Pre-rigor			In-rigor		
		Texture	Taste	Overall rating	Texture	Taste	Overall rating	Texture	Taste	Overall rating	Texture	Taste	Overall rating
4	1	82±1.8	82±3.2	83±2.5 (22)	77±0.5	79±3.3	79±3.3 (21)	80±3.4	80±2.8	80±2.8 (23)	77±3.7	85±3.0	83±3.3 (22)
16	13	80±1.0	80±1.8	80±1.3 (24)	76±3.0	75±2.3	75±2.3 (25)	75±2.6	75±2.4	74±2.1 (25)	82±2.2	80±1.9	80±1.9 (22)
28	25	70±2.5	73±1.9	73±1.9 (21)	75±1.7	75±1.6	75±1.6 (21)	71±2.0	70±2.4	70±2.0 (21)	73±1.8	73±2.3	73±1.8 (21)
59	56	59±2.0	56±2.7	56±2.7 (23)	55±1.4	61±1.9	61±1.9 (24)	62±2.5	62±2.4	62±2.4 (24)	59±2.2	53±2.3	54±1.5 (23)
88	85	53±2.1	48±2.4	50±2.2 (32)	50±2.5	45±2.5	47±2.2 (38)	53±4.1	45±2.7	48±1.9 (32)	51±1.4	49±2.9	49±3.1 (23)

Refrozen fillets, prepared from pre- and in-rigor frozen dressed fish held 9 weeks, processed and refrozen after thawing

10	1	73±4.3	76±2.9	75±1.8 (24)	76±2.6	76±2.1	76±2.1 (24)	75±2.3	77±2.4	76±2.2 (24)	73±2.4	76±3.2	75±3.2 (24)
22	13	78±2.5	74±2.3	75±2.2 (22)	70±2.1	68±2.8	68±2.8 (22)	68±2.6	70±2.4	71±2.3 (22)	74±2.7	70±2.3	70±2.2 (21)
34	25	60±1.8	61±2.4	61±2.0 (19)	54±3.1	60±2.8	59±2.9 (19)	64±3.0	66±3.3	66±3.3 (20)	65±2.1	66±2.5	66±2.5 (20)
59	50	59±1.7	57±2.0	57±2.0 (24)	60±2.3	61±2.2	62±1.8 (24)	60±2.1	61±2.3	61±2.3 (24)	56±2.6	58±1.9	58±1.5 (24)
88	79	51±1.4	45±4.1	44±2.3 (30)	49±2.5	49±2.5	49±2.3 (30)	50±1.9	45±2.2	46±2.1 (31)	44±3.4	45±3.4	47±2.9 (15)

[a] Average scores are followed by the standard error of the mean. The numbers of judgments (in parentheses) shown with the overall rating scores are common to taste and texture scores.

Other assessment (*Table VI*). The crude fat content of the fillets frozen once was3.06(±0.70)% (28) and for those frozen twice 2.57(±0.30)% (40) regardless of the method of thawing. These results may be compared with a value of 3.48(±0.88)% reported by Dyer et al. (1956) for skins-on fillets frozen once. The moisture content was 79.5(±0.49)% (20) for the fish frozen once and 79.9(±0.23)% (40) for the twice-frozen, regardless of the method of thawing.

TABLE VI. Chemical assessment, during storage at −23 C, of fillets of redfish trawled on October 2, 1964 on the Grand Bank, boated, iced before and during rigor, and stored after single and double freezing.

	Controls, and refrozen fillets prepared from dressed fish held for 3 weeks					
	Weeks in storage					
Sample[a]	Total	Refrozen	Thaw drip (% wet wt.)	Free fatty acids (% TL)	Peroxide[b]	Thiobarbituric acid units
1	6		15.5	3.5	0.54	0.035
2	↓		9.9	3.9	0.20	0.058
3	4	1	10.8	4.7	0.27	0.032
4	|	|	10.3	2.8	0.17	0.045
5	|	|	9.1	3.8	0.17	0.037
6	↓	↓	10.0	3.9	0.23	0.037
1	16		9.6	12.5	2.78	0.050
2	|		5.8	7.7	1.52	0.076
3	|	13	11.0	6.0	1.31	0.102
4	|	|	8.7	9.2	1.67	0.122
5	|	|	9.6	9.2	3.02	0.066
6	↓	↓	11.3	8.9	2.50	0.133
1	28		14.8	7.3	1.22	0.073
2	|		6.0	6.6	1.03	0.128
3	|	25	8.2	11.8	1.51	0.111
4	|	|	11.9	11.9	2.80	0.068
5	|	|	11.9	6.9	2.53	0.078
6	↓	↓	12.3	8.1	2.12	0.088
1	59		11.2	10.8	3.93	0.535
2	|		6.7	13.9	3.30	0.313
3	|	56	5.5	18.3	3.08	0.240
4	|	|	7.7	12.4	5.46	0.236
5	|	|	8.0	13.1	2.96	0.187
6	↓	↓	10.5	15.0	5.45	0.521
1	90		9.7	35.2	–	0.274
2	|		8.5	12.6	–	0.249
3	|	87	8.5	11.5	–	0.118
4	|	|	8.9	20.8	–	0.187
5	|	|	5.5	18.7	–	0.214
6	↓	↓	5.0	15.2	–	0.210

(*Continued*)

TABLE VI. Chemical assessment, during storage at −23 C, of fillets of redfish trawled on October 2, 1964 on the Grand Bank, boated, iced before and during rigor, and stored after single and double freezing. — (*Concluded*)

Controls, and refrozen fillets prepared from dressed fish held for 9 weeks.

Sample[a]	Weeks in storage: Total	Weeks in storage: Refrozen	Thaw drip (% wet wt.)	Free fatty acids (% TL)	Peroxide[b]	Thiobarbituric acid nnits
1	6		15.5	3.5	0.54	0.072
2	↓		9.9	3.9	0.20	0.064
3	10	1	10.0	7.6	1.51	0.074
4	|	|	9.5	10.9	1.25	0.036
5	|	|	9.0	7.9	1.53	0.049
6	↓	↓	8.3	6.4	0.35	0.041
1	22		9.3	5.5	1.67	0.066
2	|		8.8	4.3	1.56	0.106
3	|	13	16.2	9.8	1.48	0.064
4	|	|	9.2	6.1	1.06	0.113
5	|	|	10.9	9.8	1.10	0.048
6	↓	↓	10.6	9.4	1.25	0.048
1	34		10.3	13.3	2.10	0.151
2	|		11.0	6.5	2.43	0.296
3	|	25	7.2	9.1	2.57	0.155
4	|	|	6.9	12.1	2.88	0.325
5	|	|	12.7	8.3	3.25	0.092
6	↓	↓	10.1	8.0	2.43	0.139
1	59		11.2	10.8	3.93	0.535
2	|		6.7	13.9	3.30	0.313
3	|	50	10.4	12.9	2.36	0.162
4	|	|	10.3	10.9	2.76	0.267
5	|	|	9.7	10.2	1.25	0.253
6	↓	↓	6.5	14.2	2.71	0.456
1	90		9.7	35.2	–	0.274
2	|		8.5	12.6	–	0.249
3	|	81	6.5	22.1	–	0.083
4	|	|	8.4	15.7	–	0.274
5	|	|	8.8	11.0	–	0.141
6	↓	↓	7.3	17.8	–	0.188

[a]Samples 1 and 2, control fillets frozen once: (1) before rigor, (2) in rigor; samples 3–6, refrozen fillets: prepared from dressed fish frozen before and in rigor, processed and refrozen after thawing, in water at 15.5 C (3) before rigor, (4) in rigor, and in macrowaves (38 Mc/s) (5) before rigor, (6) in rigor.

[b]Milliequivalents per 100 g extracted fat.

The *p*H of all samples was high at the initial analysis and remained at the same level throughout the 90 weeks. The values ranged between 6.5 and 7.0, but generally they were 6.65–6.75. The different treatments did not affect *p*H.

The values (range 5.8–15.5%) of thaw-drip in the once-frozen samples were considerably higher than reported for other relatively fatty fish, e.g. water-dipped, once-frozen fillets of red snapper (*Sebastodes ruberrimus*) investigated by Boyd and Southcott (1965) produced 4% thaw-drip. In contrast to results with cod (Dyer et al., 1962; MacCallum et al., 1964a, 1966) there was no increase in the amount of thaw-drip in the present samples as the result of thawing, refreezing, and storage. An effect of state of rigor at freezing was observed, fillets frozen in rigor mortis after iced storage of parent material for 24 hr showing less thaw drip upon freezing once and storing than samples similarly prepared from pre-rigor material.

Free fatty acid values, similar for samples frozen both once and twice, increased by a factor of about 3 over the storage period of 59 weeks. The commercial, skins-on pack referred to previously (Dyer et al., 1956) showed no increase with storage at −23 C, averaging 4.6($\pm$0.86)% over a storage period of 42 weeks.

Thiobarbituric acid units increased greatly between 28 and 34 weeks independently of state of rigor at first freezing, time of thawing and refreezing, method of thawing, and number of freezings. There is an obvious relationship during storage between increasing TBA values and decreasing texture and taste scores. As shown in Table V, the latter dropped between 28 and 34 weeks storage. Up to and including 90 weeks once- and twice-frozen fish had TBA values ranging generally from 0.032 to 0.274. Values higher than the top of this range, 0.535, 0.456, 0.521, and 0.313, were obtained at 59 weeks but similarly treated packs had much lower values, 0.274, 0.188, 0.210 and 0.249, respectively, at 90 weeks. All samples were acceptable to the taste panel.

In conclusion, water- and dielectrically thawed refrozen fillets were of the same quality as control fillets frozen once. Thus, redfish of like initial condition, frozen twice, may be expected to be of good quality up to 28–34 weeks and of acceptable quality up to 88 weeks. Based on present results it would not be surprising to find grater yields in water-thawed samples than in those thawed completely in the dielectric thawer due to some losses from overheating in the latter device. While the skin of the water-thawed fish was brighter than that of the dielectrically thawed, both lots were superior to skins-on (commerial) fillets of redfish iced for some days before freezing.

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Population Dynamics of the Arcto-Norwegian Cod[1]

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ABSTRACT

By reason of its geographical distribution, the Arcto-Norwegian cod (*Gadus morhua*) supports three distinct fisheries, two feeding fisheries in the Barents Sea and at Bear Island–Spitsbergen, and a spawning fishery off the Norway coast. In the past this diversity of fishing on the one stock has made it difficult to unify all the data to give an overall description of post-war changes in the stock. In this contribution three modifications of conventional procedures are introduced which enable this to be done. These are: (i) a system of weighting the catch per unit effort data from each fishery to a level of comparability; (ii) a more rigorous definition of the effective fishing effort on each age-group; (iii) a method of estimation of the effective fishing effort on partially recruited age-groups.

Using these methods the analysis presents the effects of fishing on each fishery in the context of its effect on the *total* stock, and at the same time it indicates ways in which factors other than fishing may have influenced the apparent abundance of the stock. The treatment of the data is also used to derive estimates of spawning stock and recruitment of 3-year-old cod for subsequent analysis of stock–recruitment relationships.

INTRODUCTION

During recent years the upward trend in fish production from the North Atlantic has passed a total of 10 million tons of all marine species. Of this, 4½ million tons are gadoid species, and in 1962–63 almost 1 million tons (8% of the grand total) were taken from the single stock of Arcto-Norwegian cod (*Gadus morhua*).

This stock supports three major fisheries, two in the feeding areas of the Barents Sea, and on the Spitsbergen Shelf northward from Bear Island, and a spawning fishery in the vicinity of the Lofoten Islands. In addition to this important geographical distinction the feeding fisheries are exploited principally by trawlers whereas the spawning fishery is more heterogeneous, including trawls, gill nets, purse seine, handlines, and longlines. The Lofoten "skrei" fishery for spawning cod has been carried on for centuries by Norwegian fishermen, but it was not until the late 1920s that other European countries began regularly to exploit the same stock on its feeding grounds to the northeast. Since World War II this has continued and intensified with the expansion of the fishing fleet of the USSR, so that throughout recent history the Arcto-Norwegian cod has been one of the most important fishery resources of the North Atlantic. As such it has been the subject of a considerable amount of ecological research by fishery biologists in the USSR (see Maslov, 1960a, and

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for a bibliography of studies carried out in the USSR) and in Western Europe (Rollefsen, 1953; Trout, 1957); indeed, it was from his observations of the Lofoten fishery that Hjort (1914) first appreciated the significance of fluctuations in year-class strength to the yield of a fishery.

The recognition that the cod in these fisheries of the northeast arctic constitute a single unit stock has been the culmination of a long series of studies of the spawning biology and migration patterns of the fish in each of the three fisheries. The results of this work, which was begun by Sars in 1862, are summarized by Cushing (1966). Briefly cod eggs spawned off the Norwegian coast drift northeastward and become distributed between the Barents Sea and Spitsbergen Shelf by the North Cape and West Spitsbergen currents, respectively. The young cod adopt the demersal habit at the end of their first year and spend the early years of their life in much the same area, carrying out limited annual northeast–southwest migrations according to hydrological and feeding conditions in the areas. These fish mature at between 7 and 13 years of age and then migrate annually to the Norway coast to spawn.

In recent years the Norwegian Government has expressed concern at the downward trend in the catches of the Lofoten spawning cod fishery, and studies of the dynamics of the Arcto-Norwegian cod have been intensified with special reference to the interactions between the various fisheries. In particular all the relevant international fishery statistics and biological data have been collected and analysed by the Arctic Fisheries Working Group established by ICES (Beverton, 1960). This report outlined the magnitude and causes of mortality in the Arcto-Norwegian cod, and estimated the effects that would follow specified changes from the 110-mm minimum size for codend meshes of trawls which had been in force since 1954. As a result, the Permanent Commission recommended that, as from January 1, 1963, the minimum mesh size for codend meshes of trawls fished in this area should be raised from 110 to 120 mm (International Fisheries Convention, 1946). However, catches of Arcto-Norwegian cod continued to decline after this measure came into force, as might have been expected so shortly after the change, but nevertheless renewed concern at the uninterrupted trend of decline of the Norway coast fishery led to a reappraisal of the position by the Arctic Fisheries Working Group in 1965 (International Council for the Exploration of the Sea (ICES), 1965). The findings of this group are given in more detail in the Discussion.

The conclusions reached by the first working group depended upon conventional analyses of catch and effort statistics, in which mortality was estimated as the ratio of catch per unit effort in successive years (Ricker, 1940, 1944, 1958; Beverton and Holt, 1957) but in the 1965 reappraisal more use was made of virtual population analysis (Fry, 1949; Bishop, 1959; Jones, 1964; ICES, 1965). The initial catch and effort analyses encountered some difficulty in consolidating the statistics from the different fisheries. In this contribution these catch and effort data have been reanalysed with a different weighting system, to demonstrate their close similarity with the results subsequently obtained by the "virtual population" analysis and to clarify important un-

certainties regarding fluctuations in year-class strength. A tentative link between the catchability (q) of the stock and environmental changes is also suggested.

METHODS

It has been pointed out that the Arcto-Norwegian cod supports fisheries in three distinct geographical areas, each of which contains only a part of the total stock. As a result of this, measures of the total abundance of the stock, and hence its mortality, cannot be derived from any one fishery. Thus, whilst it has been possible to estimate rates of decrease (i.e. mortality + net migration) in each part of the stock separately, it has not previously been possible to form a satisfactory synthesis of all the data, particularly when including that of the Norway coast fishery, where changes in the exclusive territorial limits have influenced the estimates of abundance of the spawning stock based on the trawl data.

In this paper modified methods of analysis are developed which take account of the different age compositions of the catches in the different fisheries and permit the total stock to be estimated in terms of its abundance in the feeding fisheries. The results are then used to interpret the data from the Norway coast fishery, and subsequently the data from all three fisheries have been combined to analyse mortality in terms of the fluctuating abundance of the total stock when it is distributed in the feeding fisheries.

Total Catches, Catch Per Unit Effort, and the Estimation of Effective Fishing Effort in the Feeding Fisheries of the Barents Sea, and at Bear Island–Spitsbergen

Precise analyses of mortality are based upon fluctuations in the numerical strength of the stock, whichever method of analysis is adopted. The total number caught in each age-group is therefore a fundamental statistic which, in this catch/effort analysis, must be associated with estimates of fishing effort. In international fisheries such as this the efficiency and objectives of the different fleets are so varied that it is not possible to obtain an adequate measure of effort by the simple addition of the effort statistics of each fleet. In the standard notation, this limitation recognizes that

$$qf(\text{Fleet A}) \neq qf(\text{Fleet B}).$$

In order to overcome this inequality it is customary to assess the total effective fishing effort, $\bar{f}$, in terms of the fishing effort of one fleet thus:

$$\text{Total effective effort} = \frac{\text{Total international catch} \times \text{fishing effort (Fleet A)}}{\text{National catch (Fleet A)}};$$

or, alternatively,

$$\text{Total effective effort} = \frac{\text{Total international catch}}{\text{Catch per unit effort (Fleet A)}}.$$

This technique is usually applied to the total catch of all age-groups in individual calendar years, but this contains the implicit assumption that the relative catchability of different age-groups is constant between fleets, i.e.

$$\frac{qf(\text{age}_x)}{qf(\text{age}_{x+1})} \text{ Fleet A} = \frac{qf(\text{age}_x)}{qf(\text{age}_{x+1})} \text{ Fleet B},$$

and, very strictly speaking, it assumes that within each fleet

$$qf(\text{age}_x) = qf(\text{age}_{x+1}),$$

even though it takes account of the overall inequality of the two fleets.

Neither of these assumptions is accurate, because different fleets have different objectives and may concentrate on a different size-group of fish; furthermore, the catchability of two successive age-groups may differ within one fleet, and the ratio between these age-groups may be different again in another fleet. This complex can be simplified by assuming only that $qf(\text{age}_x)/qf(\text{age}_{x+1})$ is constant from year to year in one fleet, and estimating the effective effort on each age-group as

$$\text{Total effective effort (age}_x) = \frac{\text{International catch (age}_x)}{\text{National catch per unit effort (age}_x)}.$$

In this way differing objectives between fleets will be accounted for by fluctuations of the effective effort on age-groups within 1 year, and trends in q with age-groups within the selected fleet will be reflected as a trend in natural loss from the fishery with age of the fish.

In this analysis the catches per unit effort of English, German, and USSR trawlers were available, but only the English and USSR data give full coverage in all post-war years, and only the English data contain a correction for secular increases in fishing power of the trawler fleet (Gulland, 1956). The catch per 100 ton-hours of the English trawler fleet has therefore been used to derive estimates of the effective fishing effort on each age-group. The discrepancies between the English and USSR data are discussed in Appendix A.

The Estimation of Comparable Indices of Catch Per Unit Effort and Effective Effort on the "Part Stocks" in the Feeding Fisheries

Considering the effect of fishing over very short time periods the basic theory of population dynamics (Gulland, 1964a) gives the relation

$$N = \frac{A}{q} \times \frac{C}{f}$$

where N is the number of fish, A is the area occupied by these fish, C is the catch in numbers, q is their catchability, and f is the fishing effort. This may be written

$$C = \frac{f}{A} q N$$

where f/A represents the fishing intensity per unit area. It is usually taken that the annual mean distribution area of a stock is uniform, so that

$$C = q f N.$$

Hence fishing mortality is usually taken as proportional to fishing effort, rather than to fishing intensity as is required by the more rigid definition.

However, in the northeast arctic, after the spawning season, the Arcto-Norwegian stock is distributed over the Barents Sea (Region I) and on the Bear Island–Spitsbergen (Svalbard) Shelf (Region IIB), and the areas of these two regions are different, so that when fishing effort is equal in both, the fishing intensity per unit area, and hence fishing mortality, is also different. Consequently neither the catches per unit effort, nor the fishing efforts, in the two regions are directly comparable in terms representing the total stock. In order to combine the data for these two regions it is therefore necessary to weight the statistics for the difference in area of the two feeding fisheries. The second step in this analysis has therefore been to deduce values of q/A for both regions by plotting the catch per unit effort in the English trawl fisheries against the sums of effort in the preceding 3 years (Gulland, 1961). When the catch per unit effort is expressed in numbers of fish this parameter should decline exponentially with increasing effort, since $N_{x+1} = N_x e^{-z}$, provided that all year-classes are of equal strength. This last condition is not met by the data, and of course the discard rates on English trawlers would influence the plot of data grouped by years. To offset this the logarithm of the catch weight per unit effort has been plotted against 3-year sums of effort in Fig. 1. The differing slopes of the fitted regressions reflect the different fishing intensities required to generate the same proportional decline in stock in the two areas. Assuming that the other factors affecting q are constant between the two areas (e.g. the behaviour of cod with respect to the trawl) then, per 10^8 ton-hours, the areas of the two regions are in the ratio 0.2826 of Region IIB = 0.0798 of Region I, or Region I = 3.54 times Region IIB. In Fig. 2 the shaded portions in Regions I and IIB cover the fishing grounds in this ratio. The areas have been extended across Goose Bank to Novaya Zemlya in the east, and to Hope Island Deep in the northwest because, although fishable concentrations of cod may not have appeared in these localities during recent years, they still represent part of the potential range of the stock during the later part of each year, as indicated by Maslov (1960b).

The catch per unit effort and fishing effort data for the two regions can now be combined by supposing that the Bear Island–Spitsbergen "stock"

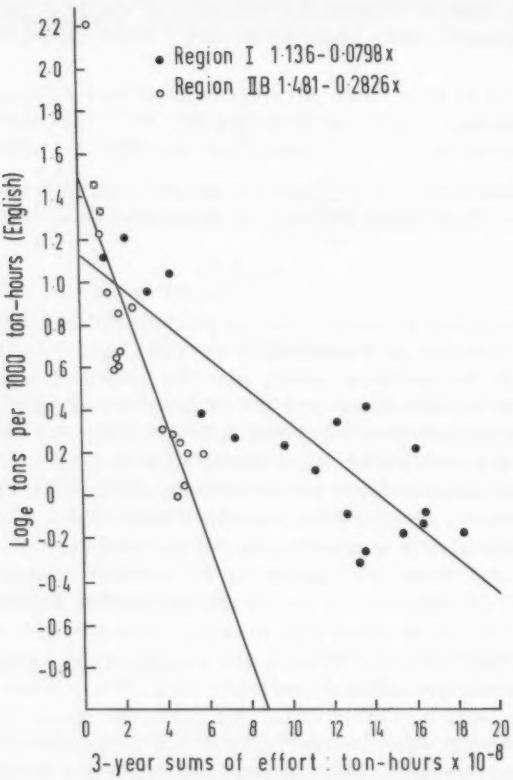

FIG. 1. The relation between stock abundance of Arcto-Norwegian cod and the amount of fishing in the Barents Sea (Region I) and Bear Island–Spitsbergen (Region IIB) fisheries.

was distributed over an area equivalent to that of the Barents Sea "stock." At Bear Island–Spitsbergen the weighted index of abundance would then become c.p.e./3.54, and fishing intensity would be fishing effort times 3.54.

THE ESTIMATION OF TOTAL ABUNDANCE OF EACH AGE-GROUP AND THE EFFECTIVE FISHING EFFORT UPON IT, INCLUDING EFFORT ON THE NORWAY COAST FISHERY

From these basic statistics of catch, fishing intensity, and index of abundance, life-history tables of individual year-classes have been reconstructed, as exemplified by that for the 1948 year-class in Table I. Columns 1–4 give the total numerical catch and catch per unit effort (English) which refer to this year-class. Column 5 is the weighted index of abundance of the total stock of

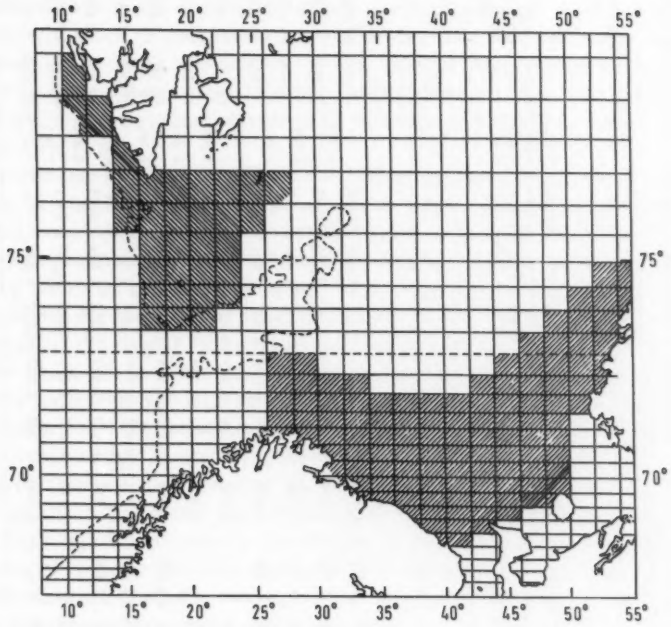

FIG. 2. The feeding distribution of the Arcto-Norwegian cod in the Barents Sea (Region I) and at Bear Island–Spitsbergen (Region IIB).

each age in the feeding fisheries, and column 6 expresses the proportion which is found in Region IIB (it is unreliable for age-groups 3–5 owing to variation in discard rates between the two areas on English trawlers). Columns 7 and 8 give the fishing effort data relevant to each age-group in each fishery, and column 9 the weighted mean fishing intensity on both feeding fisheries. Columns 1–9 thus sum up the statistics from the feeding fisheries; the contribution of the Norway Coast fishery must be added to this.

From the relationships discussed earlier, the effective fishing effort on each age-group at the Norway Coast (Region IIA) can be computed by assuming this catch as part of the total international catch of that age group. In practice it has been estimated as

$$\text{Effective effort IIA (age-group}_x) = \frac{\text{International catch IIA (age-group}_x)}{\text{Best index of abundance (I + IIB) during the spawning fishery}}.$$

Any estimate of effective effort at the Norway coast which is based upon the abundance of the age-group in the feeding fisheries in the same calender year, but subsequent to the No way coast fishery, must under-estimate the abundance in this latter fishery and hence overestimate the true effective effort.

TABLE I. Exploited life history of the 1948 year-class of Arcto-Norwegian cod (total catch in numbers × 10^{-3}: fishing effort in ton-hours × 10^{-8} and catch per effort as numbers/100 ton-hours).

		Total catch		Catch/effort (= index of abundance)			Reg. IIB stock as per cent of total	Fishing/effort		Mean fishing intensity regions I and IIB	Total catch Reg. IIA	Fishing effort Reg. IIA	Fishing intensity (adjusted)		Catch/effort (adjusted)	Total effort I + IIB +IIA	Cumulated effort	Loge catch/effort
		Reg. I	Reg. IIB	Reg. I	Reg. IIB	Total		Reg. I	Reg. IIB				Reg. IIA	Reg. I+IIB				
Age (*years*)	Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
2	1950		52															
3	1051	24 543	1 379	0.04	0.39	0.43	0.91	3.400	3.536	3.524				3.524	0.43		1.762	−0.844
4	1952	78 245	19 822	4.75	10.17	14.92	0.68	4.100	1.950	2.634				2.634	14.92	3.079	4.841	2.701
5	1953	87 383	21 814	14.46	10.94	25.40	0.43	2.600	1.994	2.339				2.339	25.40	2.486	7.327	3.235
6	1954	74 167	16 215	22.12	9.96	32.08	0.31	3.352	1.628	2.816	429	0.017	0.017	2.816	32.08	2.594	9.921	3.469
7	1955	69 163	9 473	16.97	4.02	20.99	0.19	4.074	2.357	3.745	3 898	0.086	0.086	3.745	20.99	3.366	13.287	3.045
8	1956	26 077	8 510	5.71	1.76	7.47	0.24	4.566	4.835	4.630	15 941	0.759	0.759	4.630	7.47	4.946	18.233	2.011
9	1957	6 949	3 007	1.29	0.47	1.76	0.27	5.387	6.399	5.657	8 322	1.114	1.114	2.150	4.63	4.504	22.737	1.533
10	1958	3 549	253	0.90	0.06	0.96	0.06	3.943	4.218	3.961	6 987	3.970	1.508	3.961	0.96	4.563	27.300	−0.041
11	1959	1 096	232	0.29	0.04	0.33	0.12	3.779	5.800	4.024	2 478	2.582	2.582	4.024	0.33	6.574	33.874	−1.109
12	1960	346	116	0.11		0.11		3.145		3.145	1 535	4.651	4.651	3.145	0.11	8.235	42.109	−2.207
13	1961	244		0.14		0.14		1.636		1.636	542	4.927	4.927	1.636		7.317	49.426	

In this analysis the index used is the catch per unit effort I + IIB ($year_{x-1}$), though this will tend to underestimate the effort. The best estimate would be obtained using the mean abundance of the feeding fisheries before and after each Norway coast fishery. The influence of this upon the final interpretation of the distribution of mortality between the fisheries is discussed more fully further on in this paper.

The estimates of effective effort at the Norway coast are given in Table II. These can be checked from the known maturation rate of Arcto-Norwegian cod. Within reasonable limits, determined by the selectivity of different fishing gears, all age-groups which are fully mature will be exposed to the same effective fishing effort at the Norway coast. Those age-groups which are not fully mature will be exposed to an effective effort at the Norway coast which is proportional to the degree of maturity of that age-group, and in this instance, where the units of measurement of stock abundance and fishing effort are based upon data from the feeding fishery, i.e. they measure the *total* abundance of each group, then the trends in effective effort with age at the Norway coast should correspond to the maturity ogive of Arcto-Norwegian cod.

This comparison is appended to Table II. The mean effective effort on each age-group is given for the entire sampling period, showing the increase in effort with age which reflects the degree of maturity of each age-group. In determining this mean effective effort the four estimates underlined in Table II have been excluded from the average. This can be justified by reading horizontally the effective effort in the same age-group in successive years: the values underlined show particularly high discrepancies from all other readings from that age-group, arising from poor estimates of their abundance in the feeding fisheries. The mean effort per age-group is then referred to the effort on fully matured age-groups in the spawning fishery (ca. 4.000) and compared to a percentage maturity deduced from Rollefsen's data for the years 1941–53 (Rollefsen, 1953). The similarity is illustrated in Fig. 3. There are, of course, variations in the rate of maturation of different year-classes, and in more recent years there appears to be a decrease in the mean age of maturity, but it is not clear in the English data to what extent this reflects fishing near the overwintering grounds of immature cod which are within Region IIA but not on the spawning grounds. Gulland (1964b) estimated 40% maturity at 9 years old, but he discusses various sources of bias that could also account for the discrepancy between his figure and this present estimate of 25% maturity at 9 years. For example, any estimate of maturation rate based upon data collected from the Norway coast spawning fishery may be biassed downward by the effect of fishing in the feeding areas; this mortality will lead to progressive underestimates of the true numbers of potentially late-maturing fish when they do mature and reach the spawning fishery.

The estimates of effective effort at the Norway coast have been carried over into the year-class history tables (see Table I, columns 10 and 11), with a number of minor adjustments where evidently poor estimates of abundance in the feeding fisheries (such as those referred to above) have led to dispro-

TABLE II. A comparison of effective effort on each age-group in the Norway coast spawning fishery, with the maturation rate of Arcto-Norwegian Cod.[a]

Age (*years*)	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
4															0.005		
5					0.004			0.002							0.004	0.006	
6		0.004	0.002		0.020	0.004	0.019	0.017	0.007	0.046	0.022	0.022	0.026	0.041	0.031	0.033	0.021
7	0.016	0.011	0.040	0.015	0.056	0.045	0.052	0.093	0.086	0.094	0.099	0.059	0.056	0.071	0.135	0.196	0.146
8	0.088	0.058	0.081	0.177	0.344	0.221	0.163	0.315	0.506	0.759	0.221	0.510	0.484	0.247	0.663	0.697	0.665
9	0.465	0.295	0.217	0.562	1.022	1.209	0.851	0.521	1.154	1.337	1.114	0.674	1.962	1.041	1.825	1.403	1.674
10	0.758	0.538	0.382	0.474	1.484	2.194	1.916	1.595	2.625	1.997	2.222	3.970	3.543	3.774	6.505	2.229	1.575
11	0.503	1.343	1.395	0.714	1.541	3.086	2.556	4.195	1.978	1.780	2.381	3.247	2.582	3.040	15.326	4.841	3.879
12	0.739	0.352	1.795	1.679	0.976	0.969	1.546	9.085	2.810	1.921	2.793	2.392	2.324	4.651		18.450	2.859
13	2.611	0.572	1.143	4.962	5.339	19.298	0.401	3.052	7.264	7.010	6.480	2.922	1.736	4.377		5.118	2.523

	Mean *f*/age-group	Percentage max. of 4.000	(Rollefsen, 1953)
4			
5			
6	0.019		
7	0.074	+	0.03
8	0.365	0.09	0.10
9	1.019	0.25	0.24
10	1.935	0.49	0.42
11	2.438	0.61	0.61
12	2.306	0.58	0.79
13	3.715	0.93	0.92
14+		1.00	0.99

[a]Excluding figures underlined in the section above: these are obviously anomalous.

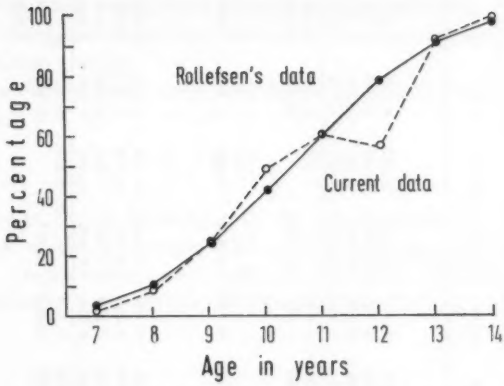

FIG. 3. A comparaison between the rate of maturation of Arcto-Norwegian cod, deduced from fishing effort data, and estimates from otolith studies described by Rollefsen (1953).

portionately high levels of effective effort at the Norway coast. For example, in column 11 of Table I the intensity of fishing on 10-year-olds is extremely high (bearing in mind the mean rate of maturation of a year-class). Reference to column 5 shows that this is generated by an apparently low estimate of abundance in the feeding fishery in 1957. An adjustment to the fishing intensity on 10-year-olds in the Norway coast fishery, in column 12, to bring it into conformity with the effort on adjacent age-groups in the same year of sampling is then carried back to indicate a more probable level of abundance of 9-year-olds in the feeding fishery (column 14). Ten of a total of 102 estimates in the age range 7–12 years have been adjusted in this way.

THE ESTIMATION OF MORTALITY RATES IN FULLY RECRUITED AGE-GROUPS (6 YEARS AND OLDER)

The estimates of total effort, and estimates of total mortality, $Z = (\text{Log}_e \text{ c.p.e.}_x - \text{Log}_e \text{ c.p.e.}_{x+1})$ derived from the data described above are given in Table III. However, for the conventional determination of the regression of Z against f only data from 1950–63 and for 6- to 10-year-old fish have been used. Data for the years 1946–49 are given in Table III but have been excluded from the calculations, owing to some doubt of the accuracy of the English catch per effort in the immediate post-war years. In the absence of a direct sampling program for length at English ports before 1950, and because of greater concentration on haddock in the Barents Sea in the immediate post-war years, the estimate of abundance of cod in the 1946–50 period given by the Arctic Working Group involves two corrections, one to adjust for changes in geographical distribution of English fishing, and a second to obtain an estimate of length composition of English catches from records of fishing by USSR

[a] Excluding figures underlined in the section above: these are obviously anomalous.

TABLE III. The correlation between total mortality and the effective fishing effort for the Arcto-Norwegian cod.

	Calendar years																
Age-groups	46/47	47/48	48/49	49/50	50/51	51/52	52/53	53/54	54/55	55/56	56/57	57/58	58/59	59/60	60/61	61/62	62/63
A	*Z (Between pairs of age-groups)*																
6 — 7	−0.056	−0.416	0.130	0.885	−0.013	0.152	0.706	0.605	0.424	0.782	0.936	0.574	0.662	1.100	0.792	0.630	1.217
7 — 8	0.823	−0.615	1.382	0.697	0.817	1.055	0.813	0.715	0.623	1.034	0.761	0.794	0.741	1.392	0.351	0.939	1.261
8 — 9	0.247	−0.195	0.363	0.556	1.026	0.875	0.805	0.939	0.729	1.501	0.478	0.494	0.936	0.926	0.344	1.158	1.687
9 — 10	1.076	1.479	0.768	1.134	1.108	1.009	0.615	0.778	0.557	1.184	0.806	1.574	1.429	0.693	1.054	1.728	1.802
10 — 11	0.630	0.888	0.305	0.888	1.252	0.720	1.236	1.085	0.538	1.689	0.542	0.405	1.068		1.387	0.792	0.693
11 — 12	0.983	1.788	0.580	1.609	2.040	1.387	1.408	1.061	1.085	2.110	1.170	1.265	1.541	1.098		0.931	2.485
12 — 13	0.272	1.207	0.761	1.166		1.163		1.058	0.944	1.140							1.179
13 — 14		0.520	0.048	1.425													
Mean:					0.734	0.773	0.735	0.759	0.583	1.125	0.745	0.859	0.942	1.028	0.635	1.114	1.492
B	*Effective fishing effort on the total stock. Ton-hours* $\times 10^{-5}$																
6 — 7	0.872	1.252	1.682	1.861	2.315	2.765	3.006	2.823	3.366	4.733	5.159	4.793	3.709	4.363	4.249	4.601	4.883
7 — 8	0.975	1.363	1.763	2.181	2.827	2.885	2.547	3.135	3.919	4.946	4.937	5.190	4.488	4.744	5.378	5.472	5.755
8 — 9	1.423	1.662	1.761	2.603	3.220	4.008	3.404	2.801	4.653	5.477	4.504	3.764	5.970	3.985	6.913	6.046	7.516
9 — 10	1.723	1.922	1.865	2.319	3.473	4.548	3.947	4.549	4.572	6.069	6.788	4.563	3.678	6.666	8.851	7.255	7.802
10 — 11	1.413	2.690	3.211	2.574	4.738	5.172	4.543	4.002	5.209	5.301	6.595	7.198	6.574		9.418	10.572	10.778
11 — 12	2.071	1.689	3.039	4.115	2.674	9.648	3.863	4.557	4.796	4.129	7.217	5.946	4.873	8.235		10.919	8.348
12 — 13	3.557	2.715	2.832	2.880		4.653		5.308	5.738	5.551							5.634
13 — 14		2.804	3.316	3.234													
Mean:					2.959	3.551	2.551	3.327	4.127	5.306	5.347	4.577	4.461	4.939	6.348	5.843	6.489

Regression formula 50/51 – 62/63. Age-group 6/7 – 9/10 $Z = 0.33 + 0.119\,f$.

trawlers. Data for older age-groups have also been excluded, owing to suggestions that over the years there may have been secular changes in the accuracy of sampling of these groups.

The relationship between total mortality, Z, and effective fishing effort, f, has the regression

$$Z = 0.33 + 0.12f$$

and is illustrated in Fig. 4, showing only the mean values for each yearof sampling. The value of the intercept, 0.33 = M, compares favourably with the values of 0.21 (6-year-olds) and 0.40 (7-year-olds) estimated by" virtual population" analysis by the Arctic Working Group (ICES, 1965).

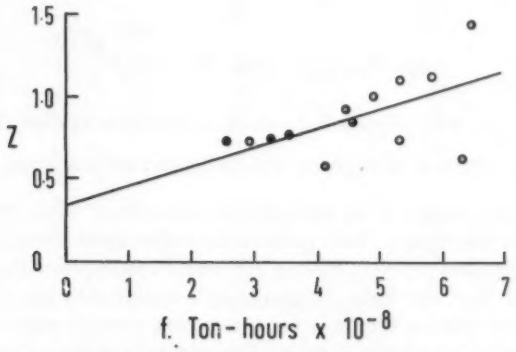

FIG. 4. The relation between fishing effort (f) and total mortality (Z) of Arcto-Norwegian cod.

THE ESTIMATION OF THE ABUNDANCE AND MORTALITY OF PARTIALLY RECRUITED AGE-GROUPS

The proportion of the total stock which is sampled by a commercial trawler is determined by the distribution of the different age-groups with respect to the trawl, and by the selectivity of the codends of the trawl. Excluding special circumstances, e.g. fisheries based upon spawning fish, it is generally assumed that during the year the stock sampled in a locality will represent all age-groups equally well. There is some doubt of this concerning the oldest age-groups of Arcto-Norwegian cod, and it is certainly untrue of the smallest cod. This, coupled with gear selection, means that younger age-groups are only partially recruited to the trawl catches, and in some fleets discarding at sea reduces still further the proportion recruited to the landings. Inspection of the English catch per unit effort data indicates that Arcto-Norwegian cod are fully recruited to the feeding fisheries at 6 years of age, i.e. $q^3 < q^4 < q^5 < q^6 = q^7 = q^8 \ldots\ldots$ However, the effect of fishing upon the partially recruited age-groups is a critically important aspect of mortality analyses which is frequently neglected

through lack of data. For example, estimates of year-class strength based upon fully recruited age-groups (6+ years) may be biassed by undetected changes in the effect of fishing upon younger age-groups (see Discussion).

Some estimate of mortality in these age-groups can be deduced from analysis of the history of individual year-classes (Table I and Appendix Table A).

From the relationship

$$N_{x+1} = N_x e^{-(qf+M)} \qquad \ldots\ldots 1$$

the usual derivation follows

$$\text{Log}_e N_{x+1} = \text{Log}_e N_x - (qf+M),$$

and hence

$$\text{Log}_e N_{x+1} = \text{Log}_e N_x - f(q+\frac{M}{f}). \qquad \ldots\ldots 2$$

This implies that a plot of the abundance of a year-class against the accumulated fishing effort to which it is exposed will be linear, with a slope $(q+\frac{M}{f})$ and an intercept $\text{Log}_e N_0$, which is an estimate of abundance when the year-class is first recruited to the fishery. This is essentially a method developed by DeLury and quoted by Ricker (1958). Taking the usual assumption that q and M will be constant with age, the form of expression 2 means that the plot will only be linear where f, the fishing effort, is constant from year to year. This limitation also applies to other methods of estimating mortalities based on annual means of pairs of years; any variation of effort between years will introduce a small error (Beverton and Holt, 1957; Paloheimo, 1961).

The further computations used in applying this technique for each year-class are added to Table I (columns 16 and 17) for the 1948 year-class. The plots for each year-class are illustrated in Fig. 5. At low levels of cumulative effort, i.e. in the younger age-groups, in each year-class the estimated abundance lies well below the regression fitted to data for fully recruited age-groups (e.g. year-classes 1950 and 1951). The estimation of effective effort on these age-groups of each year-class is not accurate, but for the present purpose of determining the relation between abundance and cumulative effort in the fully recruited age-groups this does not matter (further corrections for the partially recruited ages are introduced below). The calculated regressions for each year-class are listed in Table IV, showing the decreasing slope with increasing fishing effort per year. Mathematically some degree of curvature must be included in each regression, since there have been systematic trends in fishing effort and hence in the ratio F/F+M during the lifespan of individual year-classes, but this is barely recognizable in Fig. 5. In all year-classes the regressions are good, having approximately the same slope, as would be expected from the theoretical considerations above. It is worth pointing out here that the regressions plotted for

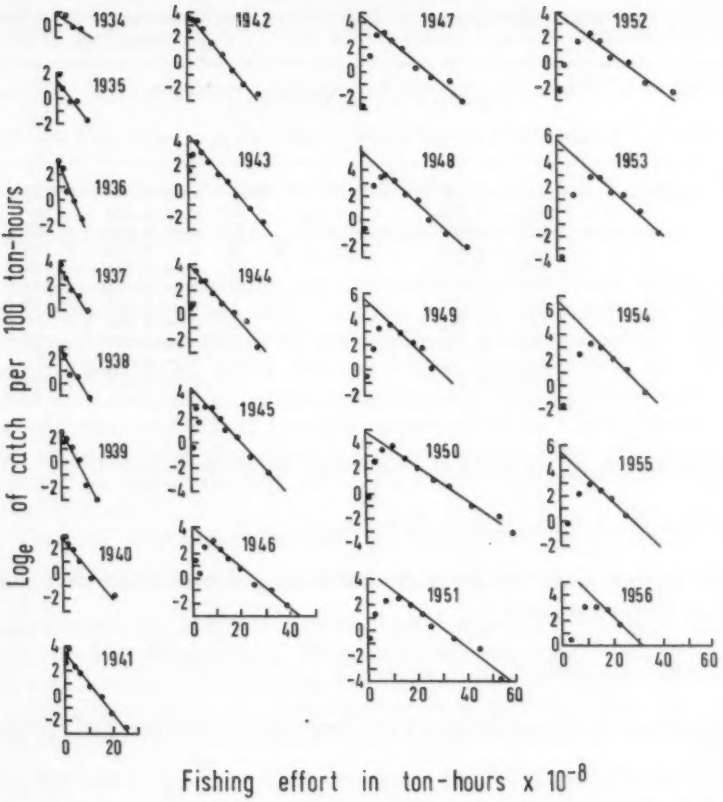

FIG. 5. The relation between catch per unit effort of Arcto-Norwegian cod and the cumulative fishing effort to which individual year-classes are exposed during their exploited life history.

data from each feeding fishery separately will not satisfy this requirement. That the weighted combined data does give a satisfactory interpretation supports the weighting factors used, and the method of treating the data.

In Table I, Appendix Table A, and Fig. 5, it has been assumed that the partially recruited age-groups are subject to the same effective effort as the fully recruited age-groups in the same year. It has already been pointed out that this must overestimate the true level of their exploitation, but the regressions in Table IV provide a method of extrapolating the abundance of younger age-groups if the effective effort to which they are exposed can be determined.

An earlier equation gave the relationship

$$\text{Log}_e N_{x+1} = \text{Log}_e N_x - f(q + \frac{M}{f}), \quad \ldots\ldots 3$$

TABLE IV. Calculation of the regression of the life history of each year-class of Arcto-Norwegian cod (see Fig. 5).

$$\text{Log}_e \text{ c.p.e.} = \text{Log}_e R_3 - f\left(q+\frac{m}{f}\right)$$

$$x = a - f\,(b)$$

1934	$x = 0.911 - 0.139\,f$	1945	$x = 4.386 - 0.223\,f$
5	$x = 1.550 - 0.284\,f$	6	$x = 4.045 - 0.167\,f$
6	$x = 2.915 - 0.500\,f$	7	$x = 4.488 - 0.165\,f$
7	$x = 3.462 - 0.332\,f$	8	$x = 5.397 - 0.186\,f$
8	$x = 2.575 - 0.336\,f$	9	$x = 5.630 - 0.189\,f$
9	$x = 2.673 - 0.389\,f$	50	$x = 4.804 - 0.133\,f$
40	$x = 2.851 - 0.242\,f$	1	$x = 4.543 - 0.149\,f$
1	$x = 3.460 - 0.245\,f$	2	$x = 3.990 - 0.147\,f$
2	$x = 4.061 - 0.243\,f$	3	$x = 5.624 - 0.178\,f$
3	$x = 4.445 - 0.231\,f$	4	$x = 6.355 - 0.197\,f$
4	$x = 3.968 - 0.221\,f$	5	$x = 5.428 - 0.184\,f$

where N_x represents the index of abundance. In back-extrapolation

$$\text{Log}_e N_x = \text{Log}_e N_{x+1} + f\left(q+\frac{M}{f}\right), \qquad \ldots\ldots 4$$

or, more strictly, where the index of abundance is related to the mid-part of a sampling year, as in Table I,

$$\text{Log}_e N_x = \text{Log}_e N_{x+1} + \tfrac{1}{2}f_{x+1}\left(q+\frac{M}{f}\right) + \tfrac{1}{2}f_x\left(q+\frac{M}{f}\right). \qquad \ldots\ldots 5$$

The abundance of an age group at the beginning of the preceding year (N_x^1) would be

$$\text{Log}_e N_x^1 = \text{Log}_e N_{x+1} + \tfrac{1}{2}f_{x+1}\left(q+\frac{M}{f}\right) + f_x\left(q+\frac{M}{f}\right). \qquad \ldots\ldots 6$$

Now $N_x = Y_{N_x}/f_x$, so that

$$\text{Log}_e N_x = \text{Log}_e Y_{N_x} - \text{Log}_e f_x, \qquad \ldots\ldots 7$$

and, substituting for $\text{Log}_e N_x$ in equation 5

$$\text{Log}_e Y_{N_x} = \text{Log}_e N_{x+1} + \tfrac{1}{2}f_{x+1}\left(q+\frac{M}{f}\right) + \tfrac{1}{2}f_x\left(q+\frac{M}{f}\right) + \text{Log}_e f_x.$$

Rearranging equation 7

$$\frac{Y_{N_x}}{N_{x+1}\, e^{\frac{1}{2}f_{x+1}\left(q+\frac{M}{f}\right)}} = f_x e^{\frac{1}{2}f_x\left(q+\frac{M}{f}\right)}. \qquad \ldots\ldots 8$$

Given estimates of Y_{N_x}, N_{x+1}, f_{x+1}, and $(q+\frac{M}{f})$, expression 8 can be solved for f_x by a graphical evaluation of the right-hand side for known values of $(q+\frac{M}{f})$. The value of f_x can then be substituted in expression 5 or 6 to obtain estimates of abundance either at the beginning or midpoint of year x. However, rapid changes in the ratio $\frac{F}{F+M}$ between years introduce nonlinearity into the regression, and in partially recruited age-groups such changes may be quite large because natural mortality will not be fully accounted for within the regression. As a result the direct substitution of f_x into expression 5 will lead to underestimates of N_x or N_x^1. But, to a close approximation, the regression method gives the value of natural mortality (distributed over the mean fishing effort per year) on the fully recruited age-groups of each year-class ($\bar{f}$), so that where there are large changes in f_x a more accurate value of $\text{Log}_e N_x^1$ can be calculated by raising the first estimate obtained from expression 5 by a proportion $M(1-f_x/\bar{f})$.

The basic data required in order to apply this technique are estimates of $(q+\frac{M}{f})$, M, N_{x+1}, and Y_{N_x}. In the present analysis all of these are available except the last, but this, the numerical yield of partially recruited age-groups, is influenced by discard rates. These are imperfectly known, but some progress can be made from an assumption that the discard rate was nil after the decline in stock abundance in the northeast arctic in 1957–58. Then, for the 1955, 1956, and 1957 year-classes the calculations described above can be carried out using the value $(q+\frac{M}{f}) = 0.184$ (see Table IV).[2] This calculation is set out in Table VA.

Column O of Table VA compares the true effective effort (g) with the effective effort on the fully recruited age-groups of the same year of sampling. This in effect is a measure of the relative availability of the age-group, and it can be seen that these year-classes give closely comparable results, with a mean 5% of 3-year-olds, 32% of 4-year-olds, and 62% of 5-year-olds.

The calculations detailed above estimate the basic availability of the partially recruited age-groups 3–5. Assuming this to have remained constant over the years it can then be used to revise the provisional effective effort attributed to these age-groups in Appendix Table A. This computation is carried out in Table VB(i). The corrections to the catch per unit effort in each age-group are set out in Table VB(ii), calculated as in Table VA, columns

[2] $(q+\frac{M}{f})$ has not been determined for the 1956 and 1957 classes, owing to lack of data from the fully recruited age-groups. Preliminary data for 1956 (see Fig. 5) indicate that the regression will be similar to that of the 1955 class, and it is reasonable to assume that the value for the 1957 class will not be very different.

TABLE Va. Calculation of the availability of partially recruited age-groups of Arcto-Norwegian cod.

		A	B	C	D	E	F (i)	F (ii)	G	H	I	J	K	L	M	N	O
		$YN \times 10^{-6}$	$\frac{YN}{f}$	f	$\frac{1}{2}f(q+\frac{M}{f})$	e^D	3) Antilog 4) L. 5) 6) ExB.	$\frac{Ax}{F(i)x+1} f_x e^D$	f_x	$G \times 0.184$	$\frac{1-fx}{f}$ $\bar{f}=4.797$	$I' \times M$ $M=0.33$	Log. $F(i)x+1$ or $Lx+1$	H+J+K	$K+\frac{L-K}{2}$	Antilog. M	$\frac{G}{C}=q$
Year-class	Age (*years*)																
1955	3	29.57		4.920			82.2	0.530	0.480	0.088	0.900	0.300	4.021	4.409	4.215	67.7	0.098
	4	65.84		4.978			55.8	1.954	1.500	0.276	0.687	0.229	3.516	4.021	3.768	43.3	0.301
	5	70.24		3.860			33.7	3.861	2.470	0.454	0.485	0.161	2.901	3.516	3.208	24.7	0.640
	6	47.65	12.29	4.260	0.3919	1.480	18.2										
1956	3	26.05		6.631			132.0	0.283	0.250	0.046	0.948	0.316	4.523	4.885	4.704	110.0	0.038
	4	94.29		4.432			92.1	1.663	1.330	0.245	0.723	0.241	4.037	4.523	4.280	72.3	0.300
	5	119.91		4.686			56.7	4.036	2.550	0.469	0.532	0.177	3.391	4.037	3.714	41.0	0.544
	6	88.84	19.47	4.593	0.4225	1.526	29.7										
1957	3	30.15		4.819			133.0	0.326	0.270	0.050	0.944	0.314	4.526	4.890	4.708	111.0	0.056
	4	137.43		4.643			92.4	2.559	1.820	0.335	0.621	0.207	3.984	4.526	4.255	70.5	0.392
	5	156.58		4.849			53.7	5.915	3.270	0.602	0.318	0.106	3.276	3.984	3.630	37.7	0.674
	6	81.01	17.09	4.761	0.4379	1.549	26.5										

TABLE Vb. (i) Correction of the effective fishing effort on age-groups 3–5 (Appendix Table A) for the effect of partial recruitment (3 = 5%, 4 = 31%, 5 = 62%).

	Calendar year																	
Age (*years*)	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
3	0.037	0.057	0.086	0.063	0.141	0.226	0.158	0.130	0.124	0.141	0.333	0.347	0.315	0.424	0.308	0.287	0.316	0.315
4	0.215	0.320	0.454	0.347	0.746	1.058	0.872	0.790	0.922	0.967	1.677	1.722	1.702	1.648	1.467	1.537	1.622	1.592
5	0.439	0.655	0.859	0.763	1.317	1.883	1.938	1.450	1.873	2.143	3.137	3.253	2.926	2.820	2.393	2.905	3.006	2.951

(ii) *Extrapolation of the log catch per unit effort of partially recruited age-groups, using the regressions from Table IV*

3.0	4.729	4.319	4.594	4.242	4.421	5.108	5.385	4.929	4.494	3.827	4.593	5.068	4.396	4.533	4.408	4.962	4.172	2.395
3.5	4.559	4.148	4.421	4.072	4.247	4.927	5.211	4.757	4.321	3.653	4.406	4.877	4.210	4.341	4.223	4.778	3.987	2.048
4.0	4.424	4.390	3.978	4.249	3.902	4.074	4.747	5.037	4.585	4.149	3.480	4.220	4.687	4.025	4.150	4.039	4.595	3.802
4.5	4.241	4.200	3.781	4.058	3.698	3.854	4.526	4.827	4.379	3.934	3.232	3.948	4.402	3.760	3.897	3.782	4.333	3.369
5.0	3.684	4.058	4.011	3.585	3.867	3.495	3.634	4.306	4.617	4.173	3.719	2.984	3.677	4.118	3.495	3.645	3.525	4.072
5.5	3.485	3.841	3.782	3.368	3.606	3.235	3.370	4.049	4.346	3.915	3.395	2.659	3.332	3.755	3.185	3.307	3.182	3.566
6.0		3.287	3.624	3.554	3.151	3.345	2.976	3.106	3.793	4.076	3.657	3.072	2.335	2.988	3.393	2.876	2.970	2.839

(iii) *Actual abundance of age-groups, estimated as the antilog of half years of* (ii) *above*

3	95.5	63.3	83.2	58.7	69.9	138.0	183.0	116.0	75.3	38.6	82.0	131.0	67.4	76.8	68.2	119.0	53.9	7.8
4	69.5	66.7	43.9	57.9	40.4	47.2	92.4	125.0	79.8	51.1	25.4	51.8	81.6	43.0	49.3	43.9	76.2	29.1
5	32.6	46.6	43.9	29.0	36.8	25.4	29.1	57.4	77.2	50.2	29.8	14.3	28.0	42.8	24.2	27.3	24.1	35.4

G–L, but using the appropriate values of $(q+\frac{M}{f})$ and $\bar{f}_x$ for each year-class. The half-yearly estimates of abundance are also calculated (Table VB(iii)), as in columns M and N of Table VA, so that these three estimates of mean annual catch per effort can be compared with the observed figures.

RESULTS

The Distribution of Fishing Mortality Between the Three Fisheries Sustained by the Arcto-Norwegian Cod

The results of the correlation between total mortality and fishing effort have already been presented in order to define a value of natural mortality for use in the determination of partially recruited age-groups. The derived value of $q = 0.12$ per 10^8 ton-hours can be combined with the fishing effort data to give idealized estimates of fishing mortality. The fishing effort data from Table VA for ages 3–5, and Appendix Table A for ages 6+ are repeated in Table VI, distinguishing between effort in the feeding fisheries of Regions I and IIB, and in the spawning fishery at the Norway coast (Region IIA), and including estimates of effort on older age-groups which are not properly sampled in the feeding fisheries although they are fished in the spawning fishery. The total fishing mortality is shown in Table VII and compared with "virtual population" estimates of fishing mortality using a value M = 0.3. The means of these two sets of estimates for age-groups 6–12, both by age-groups and by years, demonstrate the similarity of the results.

The fishing mortality as determined by this catch/effort analysis can be subdivided in a number of ways to demonstrate the effect of the different fisheries. Table VIII gives separately the effects of fishing in the feeding fisheries and the spawning fishery upon the total stock of Arcto-Norwegian cod. It has been noted earlier that the method of computing effort at the Norway coast will have underestimated its true level, and if this is taken into account a greater proportion of the total should be attributed to the spawning fishery. The difference amounts to about 25% of the value of F on the older age-groups in the Norway coast fishery, i.e. rather less than 0.1.

In Table IX the fishing mortality in the Barents Sea and at Bear Island is expressed as a proportion of that part of the Arcto-Norwegian stock which occupies each of the feeding fisheries, i.e. as if each area contained a unit stock. Thus the fishing mortality on the total stock is partitioned between the two feeding fisheries by the ratio of the catches in the two areas, and this is divided by the proportion of the stock actually in one or other of the areas (from Appendix Table A),

$$\text{i.e. } F_{\text{Reg. I}} = \text{Log}_e \left\{ e^{-F_{\text{I+IIB}}} \times \frac{Y_{N_x}}{Y_{N_{\text{I+IIB}}}} \times \frac{1}{(Y_N/f)_{\text{I}} / (Y_N/f)_{\text{I+IIB}}} \right\}.$$

TABLE VI. The effective fishing effort, by age-groups, in different fisheries for the Arcto-Norwegian cod.

Age-group	Calendar year 1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
Total stock																		
3	0.037	0.057	0.086	0.063	0.141	0.226	0.158	0.130	0.124	0.141	0.333	0.347	0.315	0.424	0.308	0.287	0.316	0.315
4	0.215	0.320	0 454	0.347	0.746	1.058	0.872	0.790	0.922	0.967	1.677	1.722	1.702	1.648	1.467	1.537	1.622	1.592
5	0.439	0.655	0.859	0.763	1.317	1.883	1.938	1.450	1.873	2.143	3.137	3.253	2.926	2.820	2.393	2.905	3.006	2.951
6		0.997	1.422	1.423	2.048	2.699	3.537	2.515	2.833	4.415	4.855	4.866	4.164	3.445	4.176	4.260	4.593	4.761
7		1.004	1.497	1.907	2.286	2.527	2.806	2.428	3.057	3.831	4.964	5.410	4.684	3.220	5.236	4.229	4.778	5.060
8		1.195	1.680	1.960	2.318	3.040	3.078	2.171	3.579	4.368	5.389	4.783	4.558	3.867	6.077	4.929	6.154	6.263
9		1.648	1.922	1.683	2.766	3.278	4.112	3.101	3.073	4.888	5.755	3.264	2.293	5.931	3.546	6.172	6.423	7.901
10		1.924	2.123	1.724	2.698	3.258	4.646	3.076	5.254	4.782	6.408	6.936	5.469	4.427	5.589	12.596	7.935	9.010
11		1.620	2.872	3.442	3.096	5.712	5.485	4.078	4.831	4.821	5.852	6.399	6.435	6.606	5.000	13.190	7.665	12.031
12		2.704	1.910	2.755	4.504	1.990	12.131	3.781	4.957	3.965	3.495	7.570	5.483	4.235	7.796	6.000	8.051	9.659
13	3.000	3.767	2.528	2.964	3.000	2.990	4.818	2.370	5.330	5.233	5.461	3.953	2.922	5.536	4.377	6.000	7.500	5.123
14	3.000	3.750	3.030	2.996	3.000	3.200	5.000	2.520	5.000	4.263	4.830	4.160	4.000	5.000	5.000	6.000	7.500	7.500
15	3.000	3.750	3.000	2.998	3.000	3.200	5.000	4.000	5.000	4.500	5.000	4.500	4.000	5.000	5.000	6.000	7.500	7.500
16	3.000	3.750	3.000	3.000	3.000	3.200	5.000	4.000	5.000	4.500	5.000	4.500	4.000	5.000	5.000	6.000	7.500	7.500
17+		3.750	3.000	3.000	3.000	3.200	5.000	4.000	5.000	4.500	5.000	4.500	4.000	5.000	5.000	6.000	7.500	7.500
Region IIA																		
6			0.004	0.002		0.020	0.004	0.019	0.017	0.007	0.046	0.022	0.022	0.026	0.041	0.031	0.033	0.021
7		0.016	0.011	0.040	0.015	0.056	0.045	0.052	0.093	0.086	0.094	0.099	0.059	0.056	0.071	0.135	0.196	0.146
8		0.088	0.058	0.081	0.177	0.344	0.221	0.163	0.315	0.506	0.759	0.221	0.510	0.484	0.247	0.663	0.697	0.665
9		0.465	0.295	0.217	0.562	1.022	1.209	0.851	0.521	1.154	1.337	1.114	0.674	1.962	1.041	1.825	1.403	1.674
10		0.758	0.538	0.382	0.474	1.484	2.194	1.916	1.595	1.811	1.997	2.222	1.508	1.311	3.774	2.602	2.229	1.575
11		0.503	1.343	1.395	0.714	1.541	3.086	2.556	2.014	1.978	1.780	2.381	3.247	2.582	3.040	3.830	3.486	3.819
12		0.739	0.352	1.795	1.679	0.976	2.994	1.546	2.635	2.810	1.921	2.793	2.392	2.324	4.651		4.428	2.859
13		2.611	0.938	1.143	1.836	2.990	3.474	2.370	3.052	3.922	4.486	3.953	2.922	1.736	4.377			2.523
14			1.443	2.046	1.499	3.221		2.520		4.263	4.830	4.160						
15				1.969	1.996	3.242												
16					1.996	3.242												
17+																		
Regions I + IIB																		
3	0.037	0.057	0.086	0.063	0.141	0.226	0.158	0.130	0.124	0.141	0.333	0.347	0.315	0.424	0.308	0.287	0.316	0.315
4	0.215	0.320	0.454	0.347	0.746	1.058	0.872	0.790	0.922	0.967	1.677	1.722	1.702	1.648	1.467	1.537	1.622	1.592
5	0.439	0.655	0.859	0.763	1.317	1.883	1.938	1.450	1.873	2.143	3.137	3.253	2.926	2.820	2.393	2.905	3.006	2.951
6	0.645	0.997	1.418	1.421	2.048	2.679	3.533	2.496	2.816	4.408	4.809	4.844	4.142	3.419	4.135	4.229	4.560	4.740
7	0.667	0.988	1.486	1.867	2.271	2.471	2.761	2.376	2.964	3.745	4.870	5.311	4.625	3.164	5.165	4.094	4.582	4.914
8	0.734	1.107	1.622	1.879	2.141	2.696	2.857	2.008	3.264	3.862	4.630	4.562	4.048	3.383	5.830	4.266	5.457	5.598
9	0.764	1.183	1.627	1.466	2.204	2.256	2.903	2.250	2.552	3.734	4.418	2.150	1.619	3.969	2.505	4.347	5.020	6.227
10	0.704	1.166	1.585	1.339	2.224	1.774	2.452	1.160	3.659	2.971	4.411	4.714	3.961	3.116	1.815	9.994	5.706	7.435
11	0.700	1.117	1.529	2.047	2.382	4.171	2.399	1.522	2.817	2.843	4.072	4.018	3.188	4.024	—	9.359	4.179	8.212
12	0.737	1.965	1.558	0.960	2.825	1.014	9.137	2.235	2.322	1.155	1.574	4.777	3.091	1.911	3.145		3.623	6.800
13		1.156	1.590	1.821	1.128		1.344		2.278	1.311	0.975			3.800				2.600
14			1.587	0.950	1.650													
15				1.029	1.512													

13																		
14			1.587	0.950	1.650													
15				1.029	1.512													

TABLE VII. Comparison of fishing mortality determined by catch/effort analysis, and by "virtual population" analysis.

	Calendar year																	
Age-group	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
	(i) **Catch/effort analysis**																	
3		0.007	0.010	0.008	0.017	0.027	0.019	0.016	0.015	0.017	0.040	0.042	0.038	0.051	0.037	0.034	0.038	0.038
4		0.04	0.05	0.04	0.09	0.13	0.10	0.09	0.11	0.12	0.20	0.21	0.20	0.20	0.18	0.18	0.19	0.19
5		0.08	0.10	0.09	0.16	0.23	0.23	0.17	0.22	0.26	0.38	0.39	0.35	0.34	0.29	0.35	0.36	0.35
6		0.12	0.17	0.17	0.25	0.32	0.42	0.30	0.34	0.53	0.58	0.58	0.50	0.41	0.50	0.51	0.55	0.57
7		0.12	0.18	0.23	0.27	0.30	0.34	0.29	0.37	0.46	0.60	0.65	0.56	0.39	0.63	0.51	0.57	0.61
8		0.14	0.20	0.24	0.28	0.36	0.37	0.26	0.43	0.52	0.65	0.57	0.55	0.46	0.73	0.59	0.74	0.75
9		0.20	0.23	0.20	0.33	0.39	0.49	0.37	0.37	0.59	0.69	0.39	0.28	0.71	0.43	0.74	0.77	0.95
10		0.23	0.25	0.21	0.32	0.39	0.56	0.37	0.63	0.57	0.77	0.83	0.66	0.53	0.67	1.51	0.95	1.08
11		0.19	0.34	0.41	0.37	0.67	0.66	0.49	0.58	0.58	0.70	0.77	0.77	0.79	0.60	1.58	0.92	1.44
12		0.32	0.23	0.33	0.54	0.24	1.46	0.45	0.59	0.48	0.42	0.91	0.66	0.51	0.94		0.97	1.16
13		0.45	0.30	0.36	0.36	0.36	0.58	0.28	0.64	0.63	0.66	0.47	0.35	0.66	0.53			0.61
14			0.36	0.36	0.36	0.38		0.30		0.51	0.58	0.50						
15				0.36	0.36	0.38												
16					0.36	0.38												
	(ii) **Virtual population analysis**																	
3																		
4		0.02	0.01	0.04	0.02	0.10	0.11	0.10	0.10	0.07	0.09	0.07	0.20	0.17	0.16	0.20	0.12	
5		0.08	0.05	0.13	0.06	0.19	0.27	0.19	0.21	0.24	0.35	0.20	0.27	0.37	0.31	0.36	0.40	
6		0.09	0.14	0.25	0.19	0.25	0.39	0.27	0.26	0.45	0.55	0.39	0.45	0.37	0.44	0.40	0.58	
7		0.16	0.36	0.28	0.29	0.39	0.43	0.26	0.34	0.46	0.50	0.45	0.43	0.37	0.38	0.44	0.52	
8		0.12	0.25	0.25	0.35	0.36	0.37	0.31	0.36	0.58	0.44	0.54	0.35	0.38	0.38	0.56	0.66	
9		0.35	0.36	0.31	0.38	0.47	0.53	0.39	0.38	0.59	0.28	0.45	0.39	0.49	0.35	0.59	0.85	
10		0.39	0.33	0.38	0.42	0.51	0.68	0.53	0.70	0.82	0.29	0.48	0.60	0.65	0.58	0.72	0.72	
11		0.61	0.46	0.50	0.67	0.66	0.92	0.66	0.88	1.20	0.26	0.61	0.61	0.50	0.73	0.64	0.92	
12		0.36	0.41	0.49	0.69	0.43	1.24	0.67	0.73	1.09	0.15	0.49	0.60	0.54	0.70	0.93	0.81	
13			0.24	0.47	0.60	0.47	0.43	0.61	0.88	0.85	0.14	0.59	0.24	0.27	0.38	0.73	0.80	
14								0.21	0.92		0.09	0.86	0.12	0.24	0.43		1.04	
15																		
16																		

Mean values, by years	Virtual pop.	Catch effort
	0.34	0.39
	0.38	0.40
	0.39	0.44
	0.45	0.45
	0.55	0.59
	0.68	0.65
	0.65	0.60

Mean values by age-groups, 6-12 only																	
Catch/effort	0.19	0.23	0.26	0.34	0.38	0.61	0.36	0.47	0.53	0.63	0.67	0.57	0.54	0.64	0.78	0.78	
Virtual population	0.30	0.33	0.35	0.43	0.44	0.65	0.44	0.52	0.74	0.35	0.49	0.49	0.47	0.51	0.61	0.72	

TABLE VIII. The fishing mortality, by age-groups, in different fisheries, as a proportion of the total stock of Arcto-Norwegian cod.

Age-group	Calendar year																
	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
(i) *Fishing mortality in regions I & IIB*																	
3	0.07	0.01	0.01	0.02	0.03	0.02	0.02	0.01	0.02	0.04	0.04	0.04	0.05	0.04	0.03	0.04	0.04
4	0.04	0.05	0.04	0.09	0.13	0.10	0.09	0.11	0.12	0.20	0.21	0.20	0.20	0.18	0.18	0.19	0.19
5	0.08	0.10	0.09	0.16	0.23	0.23	0.17	0.22	0.26	0.38	0.39	0.35	0.34	0.29	0.35	0.36	0.35
6	0.12	0.17	0.17	0.25	0.318	0.42	0.298	0.338	0.529	0.574	0.577	0.497	0.407	0.495	0.506	0.546	0.567
7	0.118	0.179	0.225	0.268	0.293	0.335	0.284	0.359	0.45	0.589	0.638	0.553	0.383	0.621	0.494	0.546	0.592
8	0.13	0.19	0.23	0.26	0.32	0.34	0.24	0.39	0.46	0.56	0.54	0.49	0.40	0.70	0.51	0.66	0.67
9	0.14	0.19	0.17	0.26	0.27	0.34	0.27	0.31	0.45	0.53	0.26	0.20	0.47	0.31	0.52	0.60	0.75
10	0.14	0.19	0.16	0.26	0.21	0.30	0.14	0.44	0.35	0.53	0.56	0.48	0.37	0.22	1.20	0.68	0.89
11	0.13	0.18	0.24	0.28	0.49	0.29	0.18	0.34	0.34	0.49	0.48	0.38	0.48	0.24	1.12	0.50	0.98
12	0.23	0.19	0.11	0.34	0.12	1.10	0.26	0.27	0.14	0.19	0.57	0.37	0.23	0.38	–	0.44	0.82
13	0.14	0.19	0.22	0.14	–	0.16	–	0.27	0.16	0.12	–	–	0.45	–	–		0.31
14		0.19	0.11	0.18	–		–		–	–	–						
15			0.12	0.12	–												
(ii) *Fishing mortality in region IIA*																	
6		–			0.002		0.002	0.002	0.001	0.006	0.003	0.003	0.003	0.005	0.004	0.004	0.003
7	0.002	0.001	0.005	0.002	0.007	0.005	0.006	0.011	0.010	0.011	0.012	0.007	0.007	0.009	0.016	0.024	0.018
8	0.01	0.01	0.01	0.02	0.04	0.03	0.02	0.04	0.06	0.09	0.03	0.06	0.06	0.03	0.08	0.08	0.08
9	0.06	0.04	0.03	0.07	0.12	0.15	0.10	0.06	0.14	0.16	0.13	0.08	0.24	0.12	0.22	0.17	0.20
10	0.09	0.06	0.05	0.06	0.18	0.26	0.23	0.19	0.22	0.24	0.27	0.18	0.16	0.45	0.31	0.27	0.19
11	0.06	0.16	0.17	0.09	0.18	0.37	0.31	0.24	0.24	0.21	0.29	0.39	0.31	0.36	0.46	0.42	0.46
12	0.09	0.04	0.22	0.20	0.12	0.36	0.19	0.32	0.34	0.23	0.34	0.29	0.28	0.56		0.53	0.34
13	0.31	0.11	0.14	0.22	0.36	0.42	0.28	0.37	0.47	0.54	0.47	0.35	0.21	0.53			0.30
14		0.17	0.25	0.18	0.39		0.30		0.51	0.58	0.50						
15			0.24	0.24	0.39												
16				0.24	0.39												
17																	

TABLE IX. Fishing mortality of Arcto-Norwegian cod in the feeding fisheries, as a proportion of the stock in each of those regions.

	Calendar year																	
Age-group	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
	(i) *Region I*																	
6		0.11	0.17	0.19	0.31	0.29	0.46	0.29	0.39	0.61	0.65	0.47	0.42	0.33	0.49	0.40	0.48	0.57
7		0.16	0.18	0.20	0.25	0.23	0.31	0.23	0.27	0.40	0.48	0.50	0.43	0.29	0.60	0.36	0.30	0.46
8		0.13	0.19	0.24	0.25	0.34	0.38	0.25	0.41	0.47	0.55	0.47	0.47	0.35	0.71	0.47	0.61	0.68
9		0.13	0.20	0.17	0.25	0.27	0.50	0.31	0.33	0.46	0.54	0.25	0.19	0.47	0.33	0.51	0.54	0.91
10		0.13	0.20	0.16	0.25	0.21	0.29	0.16	0.45	0.36	0.63	0.50	0.47	0.33	0.24	1.18	0.46	0.83
11		0.12	0.20	0.24	0.25	0.62	0.24	0.21	0.31	0.34	0.52	0.46	0.37	0.45	0.38	1.40	0.43	0.98
12		0.21	0.18	0.21	0.35	0.16	0.90	0.27	0.19	0.13	0.19	0.58	0.37	0.23	0.38		0.44	0.82
13		0.13	0.20	0.22	0.15		0.16		0.28	0.14	0.12			0.45				0.31
14			0.20	0.11	0.20													
15				0.12	0.18													
16																		
17																		
	(ii) *Region IIB*																	
6		0.16	0.16	0.14	0.21	0.33	0.19	0.23	0.17	0.23	0.34	0.75	0.75	0.81	0.36	0.79	0.63	0.44
7		0.15	0.17	0.12	0.24	0.24	0.19	0.21	0.18	0.21	0.53	0.59	0.66	0.64	0.27	0.34	0.48	0.33
8		0.16	0.16	0.16	0.29	0.27	0.21	0.21	0.23	0.31	0.59	1.06	0.56	0.64	0.52	1.16	0.81	0.61
9		0.15	0.16	0.17	0.33	0.27	0.19	0.19	0.20	0.34	0.48	0.29	0.16	0.47	0.17	0.78	1.87	0.38
10		0.16	0.16	0.16	0.45	0.27	0.36	0.09	0.40	0.23	0.63	0.09	0.59	0.83	0.10	1.82	?	?
11		0.16	0.16	0.09	0.13	0.10	0.04	0.10	0.06	0.29	0.32	0.09	0.64	0.78	0.10	0.57	1.98	?
12		0.26	0.16		0.09	0.59		0.12	0.09	0.30		0.50						
13		0.17	0.13		0.09				0.24	0.22								
14			0.16		0.07													
15																		
16																		
17																		

In general terms this shows that the effect of fishing on the Bear Island–Spitsbergen "stock" has been at least as high as that of fishing on the Barents Sea "stock" but, in terms of the effect on the total stock, the Bear Island fishery has relatively little significance, as can be judged directly from the ratios of total catches in the two areas.

A further important aspect of the data is shown in Table X, where these estimates of *fishing* mortality within each feeding fishery are compared with the estimates of *total* mortality which are obtained directly from the catch per unit effort in each region.

In Table X, column 1 gives the mean value of total mortality (Z) for each pair of age-groups, and columns 2, 3, and 4 sum the fishing mortality which should be included within that value of Z, as shown in Tables VIII and IX and recalculated as

$$\sum \frac{(6^{F}50\text{–}62 + 7^{F}51\text{–}63)}{24}.$$

This is then subtracted from the value of Z to give an implied natural mortality in each feeding fishery. The Barents Sea data give an answer close to that estimated from the grouped data for the total stock, but in the Bear Island–Spitsbergen fishery there is a clear increase with age in the apparent natural mortality. The mean value of M for this latter group is not unlike that suggested by Garrod (1964) from conventional catch/effort analysis of the Bear Island fishery alone, and it is entirely consistent with the biological background of some of the "Bear Island" cod returning to the Barents Sea after their spawning, resulting in a net loss of older fish from Bear Island to the Barents Sea grounds (Trout, 1957).

The Estimation of Discard Rates Aboard English Trawlers

In the analysis of the partially recruited age-groups of the Arcto-Norwegian cod (see Methods, section on "The estimation of the abundance and mortality of partially recruited age-groups"), estimates are given of their actual abundance in the stock (Table V). These can be compared with the catch per unit effort in English landings in order to reconstruct the trends in discard rates that have taken place during the post-war period: these are set out in Table XI. The estimated actual abundance of each age-group is first corrected for their availability to the trawl fleet, using the values of 5% of 3-year-olds, 32% of 4-year-olds, and 62% of 5-year-olds (see Table V). This is then compared with the catch per unit effort recorded by English trawlers, the difference between the two sets of figures being an estimate of the discarding of particular age-groups. These have been assessed as a numerical percentage of the total catch per unit effort of all age-groups, and as the percentage by weight, derived from an age–weight relationship for Arcto-Norwegian cod.

These estimates show very high discard rates in the 1950–55 period, with a peak of 40% by numbers and 20% by weight in 1953–54 and a second peak

TABLE X. A comparison of total mortality of Arcto-Norwegian cod deduced from catch/effort analysis in each region, and the fishing mortality in each region deduced from the fishing effort/total stock relationships (see Table IX).

Age-group	1950–51	51–52	52–53	53–54	54–55	55–56	56–57	57–58	58–59	59–60	60–61	61–62	62–63	1 Mean Z	2 I F	3 IIA F	4 ΣF	5 (M) Z−ΣF
	(i) Total mortality in Region I																	
6 – 7	−1.53	0.02	0.71	0.50	0.27	0.74	0.88	0.54	0.58	1.15	0.85	0.60	1.18	0.50	0.36	0.01	0.37	0.13
7 – 8	0.83	1.02	0.85	0.69	0.57	1.09	0.75	0.58	0.63	1.33	0.25	0.86	1.22	0.82	0.38	0.03	0.41	0.41
8 – 9	0.98	1.13	0.90	1.25	0.67	1.57	1.49	1.45	0.94	1.71	0.35	1.16	1.67	1.17	0.39	0.08	0.47	0.70
9 – 10	1.05	0.98	1.07	0.53	0.16	1.19	0.74	0.36	0.40	2.02	0.32	1.74	1.78	0.95	0.38	0.16	0.54	0.41
10 – 11	0.06	0.64	2.30	0.07	0.49	1.73	0.51	0.35	1.13	–	1.54	0.59	0.63	0.77	0.42	0.25	0.67	0.10
11 – 12	—	0.75	1.44	0.40	1.46	2.50	1.14	1.24	1.51	0.97	–	–	2.29	1.05	0.39	0.28	0.67	0.38
Mean:	0.28	0.76	1.21	0.57	0.60	1.47	0.92	0.75	0.86	1.44	0.66	0.99	1.46				Mean:	0.35
	(ii) Total mortality in Region IIB																	
6 – 7	0.76	0.69	0.69	1.19	0.91	0.95	1.03	0.67	1.15	0.77	0.67	0.74	1.35	0.89	0.41			0.48
7 – 8	0.79	1.17	0.67	0.83	1.10	0.83	0.83	1.41	1.07	2.16	1.15	1.14	1.46	1.12	0.46			0.66
8 – 9	1.23	0.48	0.55	1.66	1.44	0.86	1.32	1.73	0.91	2.64	0.32	1.13	1.75	1.23	0.49			0.74
9 – 10	1 57	1.19	1.80	1.75	0.40	0.98	1.26	2.07	0.52	2.38	1.05	1.16	1.91	1.39	0.39			1.00
10 – 11	1.79	2.45	1.49	1.81	0.91	1.39	2.02	1.34	0.27	–	0.75	–		1.42	0.45			0.97
Mean:	1.23	0.88	1.04	1.45	0.95	1.00	1.29	1.44	0.78	1.99	0.79	1.04	1.62				Mean:	0.77

TABLE XI. The estimation of discarding on English trawlers from the estimated abundance of partially recruited age-groups of Arcto-Norwegian cod (given as numbers/100 ton-hours).

	Calendar year																	
Age	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
	(i) Actual abundance (Table V) corrected for availability																	
3	6.1	4.1	5.3	3.8	4.5	8.8	11.7	7.4	4.8	2.5	5.2	8.4	4.3	4.9	4.4	7.6	3.4	0.5
4	22.9	22.0	14.5	19.1	13.3	15.6	30.5	41.3	26.3	16.9	8.4	17.1	26.9	14.2	16.3	14.5	25.1	9.6
5	20.2	28.9	27.2	18.0	22.8	15.7	18.0	35.6	47.9	31.1	18.5	8.9	17.4	26.5	15.0	16.9	14.9	21.9
	(ii) Observed abundance (c.p.e. English Appendix Table A)																	
3	5.3	1.7	0.7	4.4		0.4	0.6	0.6	0.5	0.1		0.1	0.9	1.5	4.4	2.2	1.3	0.5
4	11.1	17.3	2.2	15.6	1.5	3.5	14.9	5.1	11.0	3.8	0.8	2.7	11.5	8.9	21.4	15.6	16.2	10.3
5	14.5	34.3	17.5	30.6	5.6	11.2	18.8	25.4	26.5	28.8	11.8	4.7	13.8	23.7	18.2	22.5	28.0	30.8
	(iii) Rejected abundance (i–ii)																	
3	0.8	2.4	4.6	−0.6	4.5	8.4	11.1	6.8	4.3	2.4	5.2	8.3	(3.4)	(3.4)	(–)	5.4	2.1	−0.5
4	11.8	4.7	12.3	3.5	11.8	12.1	15.6	36.2	15.3	13.1	7.6	14.4	15.4	(5.3)	(−5.1)	(−1.1)	8.9	−0.7
5	5.7	−5.4	9.7	−12.6	17.2	4.5	−0.8	10.2	21.4	2.3	6.7	4.2	3.6	2.8	(−3.2)	(−5.6)	(−13.1)	−8.9
Total (iii)	18.3	1.7	26.6	−9.7	33.5	25.0	25.9	53.2	41.0	17.8	19.5	26.9	22.4	11.5	−8.3	−1.3	−2.1	−10.1
Total stock (i) + 6 yr+	154.8	141.7	145.7	148.5	102.7	91.6	107.2	127.6	132.2	119.1	96.8	77.1	79.5	72.6	63.3	63.7	73.6	57.0
Percentage reject	12	–	18	−6	33	27	24	42	31	15	20	35	28	16	−13	−2	−3	−17
Weight of rejects	0.017		0.024		0.032	0.019	0.017	0.045	0.040	0.014	0.017	0.021	0.014	0.009				
Weight of total stock	0.515		0.364		0.248	0.189	0.187	0.202	0.214	0.225	0.197	0.154	0.138	0.121				
Percentage reject	3		7		13	10	9	22	19	6	9	14	10	7				

in 1957 and 1958. However, the decline in discard rates to an apparently negative value in 1959 is clearly impossible and arises from the original assumption of the method, that discarding was zero for the 1955, 1956, and 1957 year-classes. Some discarding must have taken place, and so all the estimates of rejection must be slightly too low. Bearing this in mind there is a clear overall decline in discard rates through the period, with peaks during years when particularly strong year-classes have been amongst the age-groups 3–5. Thus in 1953 and 1954 the very strong 1948–50 year-classes were only partially recruited, and in 1957–58 the good 1954 year-class was just entering the fishery.

There are no quantitative records of the discard rates on English trawlers, and indeed the interpretation put forward above can only be tentative, since it refers to grouped data for both the Barents Sea and Bear Island regions. Nevertheless the percentages are of the expected order of magnitude and bear out available "hearsay" evidence.

Relationships Between the Cod Fishery and the Environment: Some Tentative Interactions

It is well known that the Arcto-Norwegian cod fishery is influenced by fluctuations in temperature. For example, Maslov (1960b) has associated year-to-year changes in the easterly summer migration of Barents Sea cod with the distribution of temperature. Konstantinov (1964) has outlined temperature-dependent relationships defining the relative success of the coastal and offshore fishery areas of the Murman Coast, and Cushing (1959) and Beverton and Lee (1965) have described various aspects of the distribution of cod and temperature on the Spitsbergen Shelf. Other workers, e.g. Kislyakov (1961), have considered the influence of temperature upon the survival of young fish.

Following the broad findings of Konstantinov it might be expected that fluctuations in temperature should influence the catchability of cod, and hence the effectiveness of fishing effort, but this cannot be defined by catch/effort analysis alone because successive annual estimates of mortality, and hence q, are interdependent. This difficulty can be overcome by using the catch/effort analysis in conjunction with the "virtual population" analysis.[3] The former gives estimates of effective fishing effort in each year (f), and the latter gives independent estimates of fishing mortality (F) in each year. The division F/f thus gives estimates of q, for each calendar year, which can be reletad to any particular feature of the environment.

In fact the mean value of q derived in this way is $q = 0.118$ per 10^8 ton-hours, very close to the value of $q = 0.12$ derived from the catch/effort analysis. However, the chronological plot of these data as the full line in Fig. 6, indicates that q may fluctuate widely, and that in the Arcto-Norwegian cod stock the value of q in the second half of the 1950s was somewhat lower than in the early years of the decade. However, as pointed out earlier, the English catch per unit

[3]This method of virtual population analysis is described and elaborated by Gulland in an Appendix to the Report of the Arctic Working Group (ICES, 1965), and since it has not been widely published the method is outlined in some detail in Appendix B of this paper.

effort data for 1946–49 are not very reliable, and over the period since 1950 there is no distinctive trend in q.

Figure 6 also shows the mean monthly anomaly (April–December) of temperatures in the 0–200-m layer at the Kola Meridian. These can be compared with the year-to-year variations of q for the whole Arcto-Norwegian stock. There is some indication that q tends to be low in warm years, e.g. 1950, 1954, and 1959, but this is not consistent and there is no correlation between the two sets of data. Indeed there is no reason to expect that fluctuations in this particular estimate of temperature should account for all the variance of q, and the comparison is given more to illustrate the value of catch and effort analysis when used in conjunction with virtual population analysis to define the variability of q.

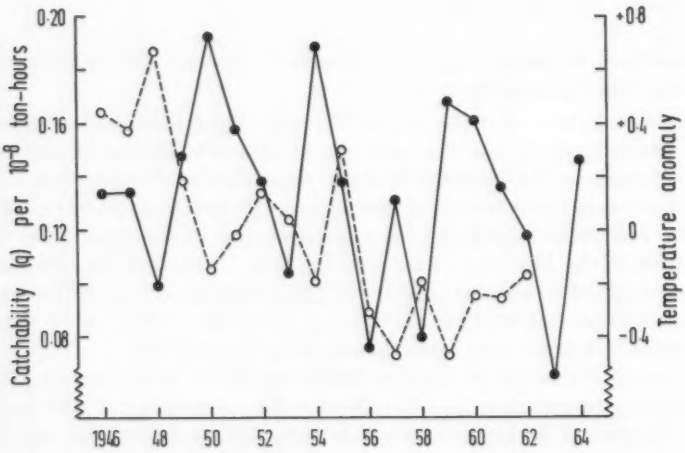

FIG. 6. Chronological changes in the catchability, q, of Arcto-Norwegian cod (full line) and in the temperature of the Kola meridian (broken line). The temperature changes are shown as the mean monthly anomaly (April–December) in the 0–200-m layer.

The increased frequency of low values of q since 1955 has an important bearing upon the interpretation of the catch/effort analysis: the fishing mortality matrices in Tables VII–IX will tend to overestimate fishing mortality during recent years. From the scale of change in q indicated in Fig. 6 the error could amount to $F = 0.10$ when estimating the real increase in fishing mortality from fishing effort between 1950 and 1963. From the point of view of assessments using the ratio $E = F/F+M$ this implies a value of 0.65 as against a value of 0.70. This is not a very important difference and it can be seen that, even taking into account the environmental influence on the catchability of cod, fishing activity has still been the most important source of mortality in recent years.

One further influence of the environment upon the fishery can be deduced from Appendix Table A. Column 6 shows the proportion of each age-group located in the Bear Island–Spitsbergen stock. Of these, the estimates for 6-year-old cod are the only accurate indication of the partition of each year-class between the two feeding fisheries: estimates of younger age-groups are influenced by the partial recruitment discussed earlier, and estimates for the older fish are biassed by the redistribution of fish following maturity. In Fig. 7 this estimated

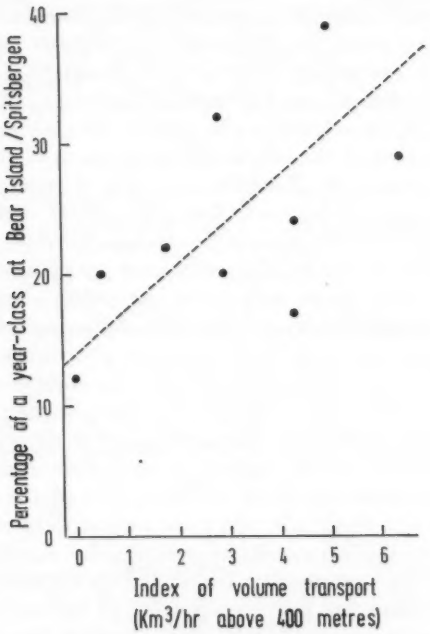

FIG. 7. The proportional distribution of year-classes of Arcto-Norwegian cod between the feeding fisheries, in relation to the volume transport in the West Spitsbergen current during the year of spawning.

proportion of 6-year-olds of each year-class which is present on the Svalbard Shelf is related to the estimated volume transport in the West Bear Island Section during the summer of the year in which they were spawned (data from Lee, personal communication). The data do not cover the entire period, but those available do show that an increased volume transport leads to relatively more young cod being drifted to the Svalbard Shelf. The analysis has not been carried further, owing to the lack of more relevant data on the differences in volume transport between the West Bear Island and Kola Sections.

The Estimation of Spawning Stock Size From the Abundance of Mature Fish in the Feeding Fisheries, and the Relationship with Year-Class Strength

The analysis so far discussed gives a comprehensive interpretation of the changes observed in the commercial population of Arcto-Norwegian cod, given a certain recruitment and the observable fishing effort. The information can also be used to investigate further the recent fluctuations in year-class strength in relation to the abundance of the spawning stock.

Hitherto this aspect of the dynamics of the stock has been complicated by the lack of accurate information concerning the abundance of the spawning stock at the Norway coast. Norwegian estimates have been biassed by unspecified increases in the fishing power of their vessels (Saetersdal and Hylen, 1964), and data from offshore trawl fisheries of England and Germany have been biassed by fluctuating objectives in the fishery. English skippers have fished further north, almost on to the overwintering grounds of the immature stock, during recent years, especially since the extension of territorial limits in 1961, and German trawlers have concentrated to a greater extent on redfish. All three sets of data may well be biassed by changes in relative distribution of a shrinking spawning stock. For example, the catch per effort recorded by Norwegian fishermen may tend to an asymptote, regardless of spawning stock size if there is some optimum density of fish for spawning purposes: as the stock is reduced the spawning zone may contract, either geographically or temporally.

The present treatment of the data permits the abundance of the spawning stock to be estimated from the catch per unit effort of the relevant age-groups in the feeding fisheries. The calculation is not given in detail, but the procedure has been to extrapolate the abundance of each year-class at successive age intervals, using the regressions given in Table IV and the effective effort per age-group in Table VI. This table also gives estimates of the fishing effort on age-groups which are not accurately represented by sampling in the feeding fisheries, but which are presumed to be subject to the same mortality as this mature age-groups which are fully represented in the spawning fishery. The permits a reconstruction of the stock in the feeding fisheries, which is then adjusted by the maturity ogive calculated earlier, to give an estimate of the spawning stock. There is no direct method of testing the accuracy of this method, beyond comparing it with other estimates derived from the Norway coast data.

The errors inherent in the Norwegian catch per unit effort data have already been mentioned, but nevertheless these should still give a representative estimate of the age composition of the spawning stock, if not of its size, bearing in mind some bias due to gear selection. Figure 8 compares the per mille age composition of Norwegian catches (from the original Working Group data) and the age composition estimated by "reconstruction" from the trawl fishery data. The similarity between the two offers some verification for the method, and, most especially, the agreement between partially matured age-groups supports the assumption that the proportion of mature fish within an age-

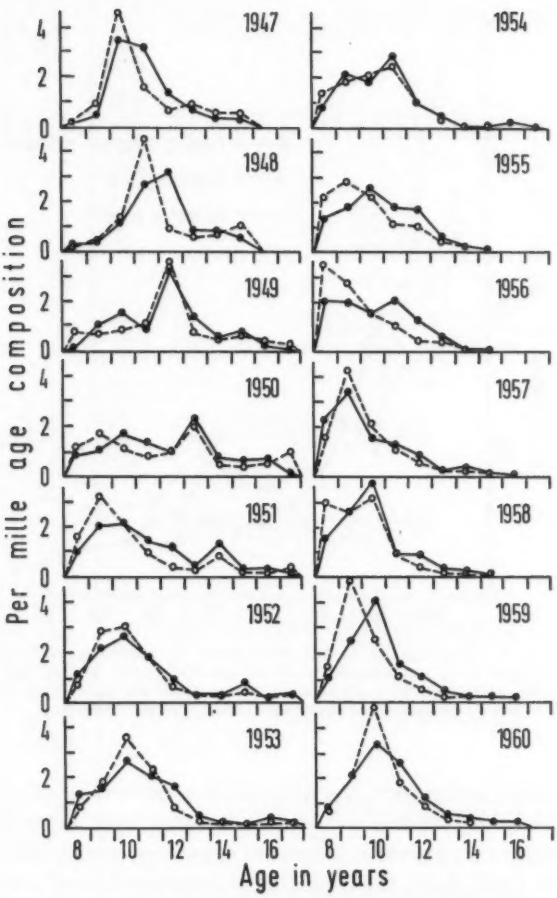

FIG. 8. A comparison between the per mille age composition of spawning cod in the Norway coast fishery, taken from the Norwegian data (broken line) and from the reconstruction of the stock from the estimated abundance of different age-groups in the feeding fisheries (full line).

group has not changed, although the observed mean may have decreased. (This was discussed earlier.) The favourable comparison in Fig. 8 also justifies the use of the mean weight per fish, as indicated by the Norwegian data, to derive an estimate of the weight per effort for this numerical reconstruction of the stock. This series of weights per unit effort has then been referred to the mean value for 1947–63, in order to compare it with the trend indicated by the Norwegian and English data from the Norway coast fishery itself (from ICES, 1965, annex 1, figure 4). The result, set out in Fig. 9, again compares favourably

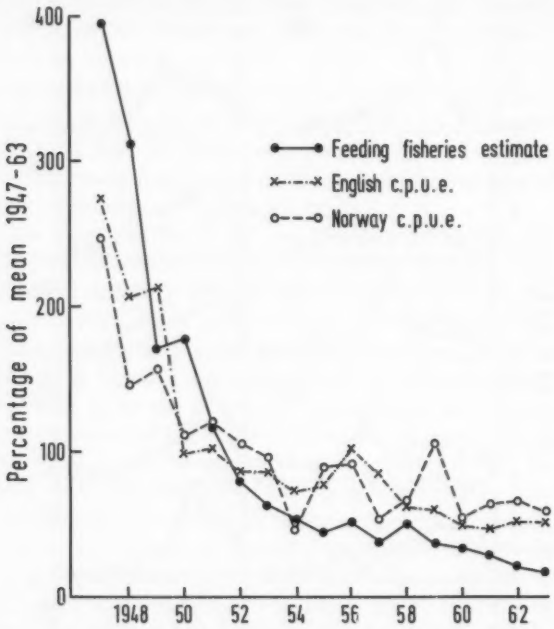

FIG. 9. The decline in the abundance of spawning cod, as deduced from the abundance of mature cod in the feeding fisheries, compared with the decline in the catch per unit effort of Norwegian and English Norway coast fisheries.

with previous data and reflects the progressive overestimate of spawning stock abundance which has taken place in the Norway coast fisheries themselves.

This procedure thus gives estimates of spawning stock which are in accord with the known facts. Now, the fecundity of female cod is proportional to their weight (A. D. Woodhead, personal communication), so that this estimated weight per effort of spawning stock is also an index of egg production (but not necessarily "egg quality") in each year.

Estimates of year-class strength have been derived earlier in the estimation of the abundance of partially recruited age-groups. These are given as logarithms in Table VA and repeated in Table XII as the relative abundance of codling at the beginning of their fourth year, i.e. 3-group. Confirmation of these estimates of year-class strength at 3 years old is shown in Fig. 10 where these data, expressed relative to the mean for 1946–60, are compared with the results of the young cod (age 0–3) surveys carried out by the USSR in the Barents Sea (Baranenkova, 1964). Bearing in mind the possible errors in the present estimates for the 1949 and 1950 year-classes, the agreement between the two sets of data is good (see below).

TABLE XII. Spawning stock size and year-class strength of Arcto-Norwegian cod.

Year-class	Present analysis: Year-class at 3 years old (Table V)	Present analysis: Spawning stock weight	Gulland (1964) year-class strength: Region I	Gulland (1964) year-class strength: Region IIB	Gulland (1964) year-class strength: IIB / 3.54	Gulland (1964) year-class strength: Adjusted I + IIB	Spawning stock: Number	Spawning stock: No. weighted by kilo/fish	Raising factors		Index of year-class	Index of spawning stock
	A	B				C		D	A/C	B/D	C × 0.56 1937–1942	D × 0.197 1937–1946
1937			96	581	164	260	104	597			146	118
1938			29	95	27	56	141	832			31	164
1939			24	25	7	31	154	916			17	180
1940			39	25	7	46	142	873			26	172
1941			62	53	15	77	126	764			43	151
1942			77	92	26	103	117	708			58	139
1943	113		66	116	33	99	106	620	1.14		113	122
1944	75		44	77	22	66	102	580	1.14		75	114
1945	99		69	52	15	84	122	706	1.18		99	139
1946	70		95	26	7	102	122	710	0.69		70	140
1947	83	153	144	48	14	158	104	628	0.53	0.244	83	153
1948	165	121	222	129	36	258	81	513	0.64	0.236	165	121
1949	218	67	279	102	29	308	65	444	0.71	0.151	218	67
1950	138	70	276	324	92	368	66	452	0.37	0.155	138	70
1951	89	45	124	268	76	200			0.44		89	45
1952	46	31	65	87	25	90			0.51		46	31
1953	99	24	105	151	43	148			0.67		99	24
1954	159	21	160	347	98	258			0.62		159	21
1955	81	17	176	136	38	214			0.38		81	17
1956	93	20									93	20
1957	82	15									82	15
1958	143	20									143	20
1959	65	18									65	18
1960	(11)	13									(11)	13
1961		11						Mean:	0.56	0.197		11
1962		8										8
1963		7							(excluding 1943–45)			7

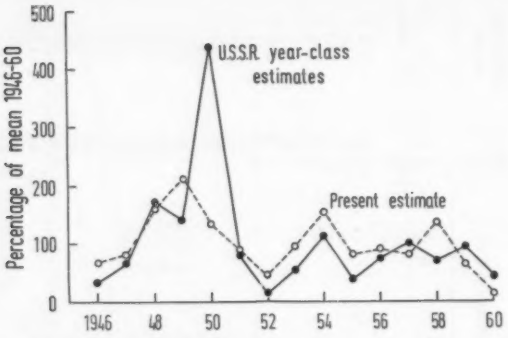

FIG. 10. A comparison of the estimated year-class strength of Arcto-Norwegian cod at 3 years old with USSR estimates from their winter surveys of 0–3 group cod in Region I.

The comparison between the estimate of spawning potential and the year-class subsequently generated from it is set out in Table XII. However, since this analysis has been based upon data from post-war years the earliest estimate of spawning stock is that of 1947, and for year-class strength that of 1943. The data have been extended using Gulland's estimates of spawning stock and year-class strength (Gulland, 1964b). His estimates of year-class strength in the two feeding fisheries are weighted for their different areas before summation to a single value for the whole stock in column C. Columns E and F determine raising factors from the years of overlap of the two series and these are used to unify Gulland's estimates with the data presented above.

The results are plotted in Fig. 11. The interpretation of this figure will be the source of further discussion, but a number of points may be made clear:

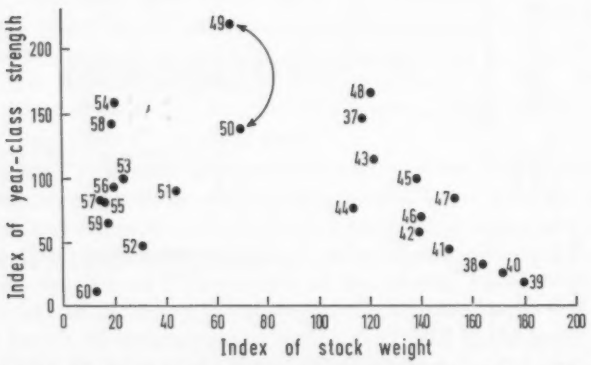

FIG. 11. The relation between spawning stock size of Arcto-Norwegian cod and the subsequent abundance at 3 years old of the resultant year-class.

(i) the raising factors are probably not very accurate, but because of the time series implicit in the results the error will have little effect on the general interpretation of Fig. 11. For example, inspection of these factors in Table XII suggests that they may be too low, so that the estimates of both spawning stock and year-class strength may be too low for the period 1937–43. (ii) Gulland's results for earlier years were based upon pre-war data and have not been included in the illustration because the original estimates of the abundance of different age-groups were not reliable, being based (a) upon scale readings — which are known to be difficult for higher age-groups, and (b) upon German length compositions converted to English catch per effort. (Trial plots of each year-class after the method developed here have shown that the fish were not fully recruited to the German landings until 7–8 years of age. This is related to market preferences (Gulland, 1964b; Lundbeck, 1964) and means that the German age composition data cannot be reliably used to estimate the composition of English landings, where year-classes were certainly fully recruited at a lower age.) (iii) The estimate of year-class strength for 1949 may be too high. The reason for this can be seen by reference to Fig. 5 and Appendix Table A. This year-class seems to "disappear" in 1959–60 and the last point in the series has rotated the regression downward in Fig. 5, giving a possible overestimate of the slope $q+\frac{M}{f}$ and hence an overestimate of the year-class strength at 3 years old. For the 1950 year-class the reverse is true. It seems possible that the acknowledgment of the 1950 group as an outstanding year-class may have led to the inclusion of some of the 1949 year-class as 1950 class, when the fish reached an age where the otolith margins become difficult to interpret. (iv) For the 1958, 1959, and 1960 year-classes these can only be preliminary estimates, pending further evidence collected since 1963.

DISCUSSION

The principal changes in the primary statistics of the Arcto-Norwegian cod fishery are shown in Fig. 12 (taken from ICES, 1965). Briefly the total catch of all regions has remained fairly steady at about 800,000 tons since the renewal of fishing after World War II, apart from two exceptional years 1955 and 1956. At the same time the proportion of the catch taken from the Norway coast fishery has decreased, and the stock abundance as an average of all areas has decreased to about 20% of its immediate post-war level. This implies that the increase in fishing effort during the same period has been wasted, insofar as it has not led to an increase in total yield. The question then arises as to what extent the trends have been generated by fishing itself, and to what extent the decline in stock abundance can be atributed to natural changes which would have taken place irrespective of changes in the amount of fishing. These questions can be answered from the foregoing analysis, the basic issue being what factors have generated the decline in stock abundance as measured by the catch per unit effort.

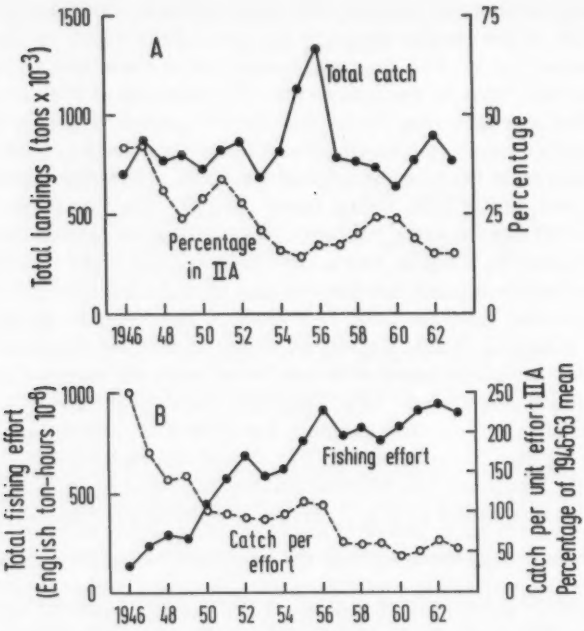

FIG. 12. A. The total catch of Arcto-Norwegian cod and the proportion caught in Region IIA. B. Total effective fishing effort on the Arcto-Norwegian cod and the trend in mean catch per unit effort.

In any fishery, changes in any one of five factors may influence the observed abundance of the stock. These factors are: (i) the fishing effort, and hence fishing mortality; (ii) the catchability of the stock; (iii) the rate of partial recruitment to the exploited stock; (iv) the absolute level of recruitment to the fishery; (v) the natural loss from the stock, either by mortality or emigration.

The changes in fishing mortality as judged from the fishing effort data are summarized in Table VII. During the war, and before the redevelopment of fishing in the Barents Sea and at Bear Island, the fishing mortality on age-groups 3–7 can be assumed to have been negligible, though, as judged from Table VIII, fishing mortality on older age-groups may have been about $F = 0.1$ as a result of fishing at the Norway coast. In the intervening years 1946–63 the fishing mortality in the feeding fisheries on both immature and mature cod has risen to about $F = 0.6$ and at the Norway coast to $F = 0.3$.

However, during the post-war period there has been a change in the catchability of Arcto-Norwegian cod as measured by the English trawler fleet. This was illustrated in Fig. 6. It is possible that since 1956 the value of q has been lower, though it cannot be shown whether this reflects a change in the biological

characteristics of the stock, or in the efficiency of the English fleet. This change can also be seen in the mean values of fishing mortality of 6- to 12-year-old cod derived from the catch/effort analysis and virtual population analysis and given in Table VII. From this evidence it is concluded that in recent years estimates of fishing mortality derived from English data are slightly too high.

The analysis of mortality in the partially recruited age-groups is obscured by trends in the discard practices aboard English trawlers. It has been suggested that there has been a tendency to fish more for smaller cod during recent years, as the older age-groups have become less abundant, thus increasing the rate of recruitment. However, an assumption that the rate of recruitment of each age-group remained constant throughout the period implies discard rates which are consistent with what is known to have occurred (see Table V). It therefore seems more probable that the apparent increase of fishing on small cod is a change in recruitment to English landings and not to the exploited stock, since the observed changes in the stock can be explained without postulating a change in recruitment to the catches.

On the other hand the effects of (random) variations in recruitment to the stock are particularly evident in the peak landings of 1955 and 1956 of Fig. 12. These were associated with the 1948–50 year classes, which were exceptionally good (see Table XII) and which were fully recruited to the fisheries as 5- to 7-year-olds during the mid 1950s. Subsequent year-classes have on the whole been smaller, but not less than the year-classes of the pre-1948 period. Consequently, though there are indications of complex stock–recruitment relations in Fig. 11, during the time period considered here they have not contributed a great deal to the decline in stock abundance. This may be qualified by the corollary that a decline in abundance has resulted from recent year-classes being less abundant than those of 1948–50, but it is not yet certain to what extent, if any, these good year-classes were themselves generated by fishing. Compared with the pre-1948 period, recruitment to the stock has, if anything, improved.

A comparison between stock abundance in 1948 and in 1963, i.e. outside the period of influence of the 1948–50 year-classes, shows that the recently low abundance is not primarily related to a serious decline in the absolute level of recruitment.

Finally it is noted that it has not been possible to detect any change in natural loss from the stock. The pattern of recapture of fish marked in the Arcto-Norwegian cod area has remained typical of the migrations deduced in earlier years (Cushing, 1966), and there is no clear indication in Fig. 4 that the natural mortality in the stock as a whole should lie on a different regression for more recent years, when high levels of fishing effort have been recorded.

Thus, during the post-war years up to 1960, and excluding 1948–50, recruitment to the Arcto-Norwegian cod stock has remained more or less steady. Similarly there has been no marked change in the rate of recruitment of codling to the exploited stock and no changes in natural loss have been detected apart from the suspected change in catchability discussed above. It is therefore

concluded that the changes outlined in Fig. 12 can be almost entirely attributed to the effect to fishing itself.

SUMMARY

1) The population dynamics of the Arcto-Norwegian cod are analysed by the reconstruction of changes that have taken place in the stock as measured in the feeding fisheries of the Barents Sea, and at Bear Island–Spitsbergen.
2) Three modifications of analytic technique are introduced:
   i) the measurement of variations in concentration of fishing upon different age-groups of cod within the same year;
   ii) the adjustment of catch per unit effort and fishing effort to offset differences in fish density and fishing intensity per unit area between the Barents Sea and Bear Island–Spitsbergen fisheries;
   iii) the development of a method for estimating the abundance and effective fishing effort on partially recruited age-groups, and which at the same time gives improved estimates of year-class strength at recruitment.
3) The analysis of catch/effort data gives values ($M = 0.33$ and $q = 0.12$) which are the same as those determined by the alternative virtual population analysis.
4) The catch/effort analysis detects emigration of maturing cod from the Bear Island fishery. Previously this has only been identified in experiments where fish tagged at Bear Island have been returned from the southeast Barents Sea.
5) The determinations of partial recruitment and the comparison of the actual and observed abundance of these age-groups in English data imply certain changes in the discard rates in this fleet. These are shown to be in accordance with available evidence.
6) The combination of results from the catch/effort analysis and "virtual population" analysis permits the determination of changes in catchability between calendar years. Lower values of q have been more frequent since 1956.
7) Evidence is presented to show that, in years of high volume transport in the West Spitsbergen current, a greater proportion of a year-class is drifted on to the Svalbard Shelf.
8) The method of estimating the total abundance of Arcto-Norwegian cod in its feeding fisheries permits the reconstruction of the Norway coast spawning stock. This reconstruction illustrates changes in the spawning stock which, though previously suspected, had not been detected owing to various sources of bias in the data collected in the Norway coast fishery itself.
9) The new estimates of year-class strength, and the reconstruction of the spawning stock, are related to show a time series of changes in both aspects of the stock.
10) Post-war changes in the fisheries are discussed in relation to the implications of the changes in fishing effort, catchability, partial recruitment, and year-class strength which have been demonstrated during the analysis.

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APPENDIX A

A Comparison of English and USSR Catch Per Unit Effort Data

The key-statistics of the catch/effort analysis are the total international catch of each age-group, by numbers, and the catch per unit effort in the feeding fisheries. In this latter statistic there is a choice between the USSR catch per hour, and the English catch per 100 ton-hours, the fishing by other countries not having been sufficiently representative at both the Barents Sea and at Bear Island–Spitsbergen throughout the period. The analysis has been based upon the English data because it has the additional advantage of having incorporated in it a correction for secular changes in fishing power that have taken place as the size of trawlers has increased. This is not available for USSR data.

In order to check any major discrepancies between the English and USSR data the catches per effort of the two countries for the Barents Sea have been compared in Appendix Table B.

If the USSR and English data were uniform then the ratio for each age-group should remain constant. Looking first at the best sampled age-groups (6–10) this ratio is satisfactorily constant within years, and discrepancies in older age-groups are in part due to the "rounding" of estimates of abundance which are very low. However there are systematic changes between years, particularly during the period 1954–58, as shown by the mean ratio of all groups over 6 years old. This was a period of expansion of the USSR fishing in the Barents Sea, so the trend may be associated with increased fishing power of the newly built trawlers. There is an additional possible source of bias in USSR statistics in that the main objective of their fishery was switched to redfish in the late 1950s, with an apparent relative underestimate of the catch per effort of cod during these years. It would appear from the increase in the ratio at the end of the period that the USSR fleet has again fished more intensively for cod as redfish catches have declined.

It is felt that these trends in fleet expansion and fleet objectives in the USSR data will explain the major discrepancies between the two sets of data.

APPENDIX B

Gulland's Method of Virtual Population Analysis

The population (r) of a year-class at the end of a year can be expressed as a proportion of the catch during the year:

$$ {}_{x}r_{n} = \frac{{}_{x}N_{n+1}}{{}_{x}C_{n}} = \frac{{}_{x}N_{n}e^{-(F+M)}}{{}_{x}N_{n}\ (F/(F+M))\ (1-e^{-(F+M)})} \qquad (A) $$

where F represents the fishing mortality on year-class x at t years old in year n. Thus if the expression

$$ \frac{(F+M)e^{-(F+M)}}{F(1-e^{-(F+M)})} $$

is tabulated at a known value of M for a range of values of F, ${}_{t}F_{n}$ can be determined immediately once ${}_{x}r_{n}$ is known.

The virtual population (V) of a year-class can be defined as

$$ {}_{x}V_{n+1} = {}_{x}E_{n+1}\ {}_{x}N_{n+1} \qquad (B) $$

so, from A,

$$ {}_{x}r_{n} = \frac{{}_{x}V_{n+1}}{{}_{x}E_{n+1}\ {}_{x}C_{n}} = \frac{1}{{}_{x}E_{n+1}}\left(\frac{{}_{x}V_{n+1}}{{}_{x}V_{n} - {}_{x}V_{n+1}}\right) = \frac{1}{{}_{x}E_{n+1}}\left(\frac{{}_{x}S_{n}}{1-{}_{x}S_{n}}\right) \qquad (C) $$

Thus ${}_{x}r_{n}$ is a simple fraction of the apparent survival during year n (as estimated from virtual populations) and the exploitation ratio ${}_{x}E_{n+1}$ applicable to the fish of the x year-class alive at the end of year n.

The exploitation ratio ${}_{x}E_{n}$ applicable to fish at the beginning of the year n will be the sum of the proportions of fish alive at the beginning of the year which are caught during that year and in subsequent years;

$$ {}_{x}E_{n} = \frac{{}_{t}F_{n}}{{}_{t}F_{n} + M}\ (1-e^{-({}_{t}F_{n}+M)}) + e^{-({}_{t}F_{n}+M)}\ {}_{x}E_{n+1} \qquad (D) $$

Thus, from the determined value of M, and an assumed value of ${}_{x}E_{n+1}$ for the final year in which a year-class contributes to the catches, successive values of ${}_{x}r_{n}$, ${}_{t}F_{n}$, ${}_{x}E_{n}$, ${}_{x}r_{n-1}$, ${}_{t-1}F_{n-1}$, etc. can be estimated.

APPENDIX TABLE A. The exploited life history of successive year-classes of Arcto-Norwegian cod.

Column: 1 Total catch in numbers, Region I, $\times 10^{-3}$
2 Total catch in numbers, Region IIB, $\times 10^{-3}$
3 No/100 ton-hours, English, Region I
4 No/100 ton-hours, English (corrected), Region IIB
5 Total No/100 ton-hours (3 +4)
6 Proportion of each age-group in Region IIB (col.4/col.5)
7 Fishing effort, ton-hours $\times 10^{-3}$, Region I
8 Fishing effort, ton-hours $\times 10^{-3}$, Region IIB
9 Total fishing effort. Calculation as in text

Column: 10 Total catch in numbers, Region IIA, $\times 10^{-3}$
11 Fishing effort, ton-hours $\times 10^{-3}$, Region IIA (for derivation see text)
12 Corrected fishing effort in Region IIA
13 Corrected fishing effort in feeding fisheries (from col. 9)
14 Corrected catch per unit effort (from col. 5)
15 Total fishing effort for pairs of years as $\frac{(9x + 9x+1)}{2} + 12x$
16 Cumulative fishing effort to the midpoint of each year
17 Log_e catch per unit effort (col. 14)

Year-class	Sample year	1–	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1934	1946	634	1 036	0.95	1.32	2.27	0.58	0.670	0.785	0.737			2.611	0.737	2.27		0.368	0.820
	1947	1 330	671	1.23	0.50	1.73	0.29	1.081	1.342	1.156	5 927	2.611	1.443	1.156	1.73	3.557	3.925	0.548
	1948	940	298	0.56	0.22	0.78	0.28	1.679	1.354	1.587	2 497	1.443	1.969	1.587	0.78	2.804	6.729	−0.248
	1949	623	68	0.44	0.05	0.49	0.10	1.416	1.360	1.410	1 536	1.969	1.996	1.029	0.67	3.277	10.006	−0.400
	1950	156	—	0.01	—	0.01	—	15.600		15.600	1 335	2.725				10.310		
											606							
1935	1946	2 426	1 579	3.62	2.10	5.72	0.37	0.670	0.752	0.700			0.739	0.700	5.72		0.350	1.744
	1947	2 055	2 151	1.90	1.61	3.51	0.46	1.082	1.336	1.198	4 229	0.739	0.938	1.965	2.14	2.071	2.421	0.761
	1948	787	230	0.47	0.17	0.64	0.27	1.675	1.353	1.590	2 007	0.572	2.046	1.590	0.64	2.715	5.136	−0.446
	1949	575	—	0.23	—	0.23	—	2.500	—	2.500	1 309	2.046	1.996	0.950	0.61	3.316	8.452	−0.494
	1950	263	36	0.04	—	0.04	—	6.575	—	6.575	1 221	5.309	3.242	1.512	0.17	3.227	11.679	−1.772
1936	1946	8 146	5 236	12.15	6.84	18.99	0.36	0.670	0.766	0.704				0.704	18.99		0.352	2.943
	1947	9 555	1 778	8.83	1.33	10.16	0.13	1.083	1.337	1.117	9 558	0.503	0.503	1.117	10.16	1.413	1.765	2.313
	1948	1 732	901	1.03	0.66	1.69	0.39	1.682	1.365	1.558	3 576	0.352	0.352	1.558	1.69	1.689	3.454	0.525
	1949	1 438	10	0.79	—	0.79	—	1.821	—	1.821	1 931	1.143	1.143	1.821	0.79	2.832	6.286	−0.236
	1950	265	47	0.06	0.01	0.07	0.14	4.418	4.700	4.460	1 184	1.499	1.499	1.650	0.19	3.234	9.520	−1.661
1937	1946	11 199	16 921	16.72	20.08	36.80	0.55	0.670	0.843	0.764				0.764	36.80		0.382	3.605
	1947	9 083	5 553	8.38	4.17	12.55	0.33	1.084	1.332	1.166	27 884	0.758	0.758	1.166	12.55	1.723	2.105	2.529
	1948	4 579	3 309	2.73	2.43	5.16	0.47	1.677	1.362	1.529	16 853	1.343	1.343	1.529	5.16	2.690	4.795	1.641
	1949	2 674	101	1.02	0.05	1.07	0.47	2.622	2.020	2.594	9 262	1.795	1.795	0.960	2.89	3.039	7.834	1.061
	1950	939	76	0.16	0.02	0.18	0.11	5.867	3.800	5.638	5 309	4.962	1.836	1.128	0.90	2.880	10.714	−0.105
	1951	291																
1938	1946	5 422	3 551	8.10	4.14	12.24	0.34	0.670	0.858	0.734				0.734	12.24		0.367	2.501
	1947	6 168	5 110	5.70	3.83	9.53	0.40	1.082	1.334	1.183	5 694	0.465	0.465	1.183	9.53	1.423	1.790	2.254
	1948	2 539	901	1.51	0.66	2.17	0.30	1.682	1.365	1.585	5 129	0.538	0.538	1.585	2.17	1.922	3.712	0.775
	1949	3 275	31	1.60	—	1.60	—	2.047	—	2.047	3 027	1.395	1.395	2.047	1.60	3.211	6.923	0.470
	1950	768	140	0.17	0.01	0.18	0.06	4.517	14.000	5.044	2 687	1.679	1.679	2.825	0.32	4.115	11.038	−1.139
	1951	25	22	—							961	5.339	2.990					
1939	1946	5 859	2 187	9.48	2.59	12.07	0.21	0.618	0.844	0.667				0.667	12.07		0.333	2.491
	1947	5 194	671	4.80	0.50	5.30	0.09	1.082	1.342	1.107	1 067	0.088	0.088	1.107	5.30	0.975	1.308	1.668
	1948	8 970	1 508	5.34	1.10	6.44	0.17	1.680	1.371	1.627	1 562	0.295	0.295	1.627	6.44	1.662	2.970	1.863
	1949	4 [illegible]	76	2.94	0.05	2.99	0.02	1.336	1.520	1.339	2 439	0.382	0.382	1.339	2.99	1.865	4.835	1.095
	1950	2 [illegible]	522	1.90	0.03	1.93	0.02	1.343	1.633	1.344	3 302	0.474	0.474	1.344	1.93	2.424	6.759	0.657
	1951	2 448	55	1.97		2.00	0.01	1.343	1.633	1.344	1 452	0.543	0.541	4.171	0.64	2.224	8.738	1.096
	1952	1 438	126	0.93		0.93	—	1.546	—	1.550	1 939	0.969	2.994	9.648	11.335	4.738	6.507	0.806
	1953	94		0.04		0.04		1.546		1.546								

1939	1946	5 859	2 187	9.48	2.59	12.07	0.21	0.618	0.844	0.667					0.667	12.07	0.975	0.333	2.491
	1947	5 194	671	4.80	0.50	5.30	0.09	1.082	1.342	1.107	1 067	0.088	0.088		1.107	5.30	1.662	1.308	1.668
	1948	8 939	1 508	5.34	1.10	6.44	0.17	1.580	1.371	1.627	1 562	0.295	0.295		1.627	6.44	1.865	2.970	1.863
	1949	2 927	76	2.94	0.05	2.99	0.02	1.336	1.520	1.339	2 452	0.382	0.382		1.339	2.99	2.854	4.835	1.095
	1950	2 415	325	2.09	0.13	2.22	0.07	2.343	1.857	2.224	3 302	0.474	0.474		2.224	2.22	4.738	6.597	0.606
	1951	2 143	97	2.07	0.03	2.10	0.01	2.350	1.833	2.350	3 452	1.541	1.541		2.071	9.04	9.648	13.335	−0.446
	1952	1 438	126	0.93		0.93	—	1.546	—	1.546	1 939	0.969	2.994		9.137	0.16		20.983	−1.833
	1953		94	0.04		0.04	—	2.350	—	2.350	373	0.401	2.370						
	1954		72	14	—		—	—	—		168	4.200							
1941	1946	4 573	5 897	7.84	6.95	14.79	0.47	0.584	0.849	0.708					0.708	14.79	0.852	0.354	2.695
	1947	21 361	5 332	22.79	4.00	26.79	0.15	0.938	1.333	0.997					0.997	26.79	1.252	1.206	3.288
	1948	52 607	7 605	35.00	5.57	40.57	0.14	1.505	1.365	1.486	304	0.011	0.011		1.486	40.57	1.763	2.458	3.704
	1949	17 697	1 491	9.08	1.13	10.21	0.11	1.948	1.320	1.879	3 272	0.081	0.081		1.879	10.21	2.603	4.221	2.322
	1950	10 844	2 050	5.06	0.79	5.85	0.13	2.143	2.595	2.204	5 740	0.562	0.562		2.204	5.85	3.473	6.824	1.766
	1951	3 069	356	1.77	0.16	1.93	0.08	1.734	2.225	1.774	8 681	1.484	1.484		1.774	1.93	5.172	10.297	0.658
	1952	1 900	356	0.93	0.01	0.94	0.01	2.042	35.600	2.399	5 957	3.086	3.086		2.399	0.94	3.863	15.469	−0.062
	1953	504	10	0.22	0.01	0.23	0.04	2.291	1.000	2.235	1 453	1.546	1.546		2.235	0.23	5.308	19.332	−1.470
	1954	143	43	0.03	0.01	0.04	0.25	4.767	4.300	4.650	702	3.052	3.052		2.278	0.08		24.640	−2.528
	1955	18	15		0.01	0.01					348	8.700	4.263						
1942	1946	4 562	2 639	7.93	3.14	11.07	0.28	0.575	0.841	0.651					0.651	11.07	0.853	0.325	2.407
	1947	20 818	15 444	22.79	11.56	34.35	0.34	0.914	1.336	1.056					1.056	34.35	1.241	1.178	3.535
	1948	35 586	8 810	24.84	6.45	31.29	0.21	1.431	1.366	1.418	141	0.004	0.004		1.418	31.29	1.682	2.419	3.444
	1949	42 269	9 150	20.08	7.46	27.54	0.27	2.105	1.226	1.867	1 239	0.040	0.040		1.867	27.54	2.181	4.101	3.314
	1950	23 062	6 265	11.03	2.67	13.70	0.19	2.091	2.346	2.141	4 863	0.177	0.177		2.141	13.70	3.220	6.282	2.617
	1951	9 354	1 722	4.13	0.78	4.91	0.16	2.265	2.208	2.256	14 003	1.022	1.022		2.256	4.91	4.548	9.502	1.591
	1952	3 732	657	1.55	0.24	1.79	0.13	2.408	2.738	2.452	10 769	2.194	2.194		2.452	1.79	4.543	14.050	0.582
	1953	905	145	0.15	0.05	0.20	0.25	6.034	2.900	5.250	4 575	2.556	2.556		1.522	0.52	4.557	18.593	−0.654
	1954	323	150	0.10	0.01	0.11	0.09	3.230	15.000	4.300	1 817	9.085	2.635		2.322	0.18	5.738	23.150	−1.715
	1955	76	38	0.03	0.01	0.04	0.25	2.533	3.800	2.850	799	7.264	3.922		1.311	0.07		28.888	−2.659
	1956	27		0.02		0.02		1.350	—	1.350	420	10.500	4.830						
1943	1946	2 845	220	5.00	0.27	5.27	0.05	0.569	0.815	0.582					0.582	5.27	0.774	0.291	1.662
	1947	13 161	3 893	14.63	2.67	17.30	0.15	0.899	1.335	0.966					0.966	17.30	1.176	1.065	2.851
	1948	16 283	7 928	11.67	5.79	17.46	0.33	1.395	1.369	1.386					1.386	17.46	1.406	2.241	2.862
	1949	54 116	21 635	34.84	18.46	53.30	0.35	1.553	1.173	1.421	39	0.002	0.002		1.421	53.30	1.861	3.647	3.976
	1950	34 829	15 163	15.26	6.74	22.00	0.31	2.281	2.250	2.271	825	0.015	0.015		2.271	22.00	2.827	5.508	3.091
	1951	19 076	7 121	6.66	3.06	9.72	0.31	2.865	2.327	2.696	7 566	0.344	0.344		2.696	9.72	4.008	8.335	2.274
	1952	8 477	3 280	2.16	1.89	4.05	0.47	3.925	1.735	2.903	11 749	1.209	1.209		2.903	4.05	3.947	12.343	1.399
	1953	2 053	484	0.74	0.31	1.05	0.30	2.774	1.561	2.416	7 762	1.916	1.916		1.160	2.19	4.002	16.290	0.784
	1954	1 785	301	0.69	0.05	0.74	0.07	2.586	6.020	2.817	4 405	4.195	2.014		2.817	0.74	4.796	20.292	−0.301
	1955	270	37	0.16	0.01	0.17	0.06	1.687	3.700	1.805	2 080	2.810	2.810		1.155	0.25	5.551	25.088	−1.386
	1956	75	—	0.02	—	0.02		3.750		3.750	1 207	7.010	4.486		0.975	0.08		30.639	−2.526
	1957	9	7	—	—														
1944	1947	1 484	22	1.67		1.67	—	0.889	—	0.889					0.889	1.67	1.131	0.444	0.513
	1948	1 937	1 162	1.41	0.77	2.18	0.35	1.374	1.370	1.373					1.373	2.18	1.301	1.575	0.779
	1949	24 200	13 469	18.39	12.24	30.63	0.40	1.316	1.100	1.230					1.230	30.63	1.639	2.876	3.421
	1950	17 878	16 935	6.49	9.07	15.56	0.58	2.300	1.868	2.048					2.048	15.56	2.315	4.515	2.747
	1951	28 214	10 959	11.58	4.26	15.84	0.27	2.435	2.572	2.471	879	0.056	0.056		2.471	15.84	2.885	6.830	2.760
	1952	13 147	2 571	4.18	1.32	5.50	0.24	3.145	1.948	2.857	3 500	0.221	0.221		2.857	5.50	3.404	9.715	1.705
	1953	4 289	1 246	1.70	0.76	2.46	0.31	2.523	1.640	2.250	4 682	0.851	0.851		2.250	2.46	4.549	13.119	0.900
	1954	3 689	446	1.00	0.13	1.13	0.12	3.689	3.430	3.659	3 924	1.595	1.595		3.659	1.13	5.229	17.668	0.122
	1955	1 743	134	0.61	0.05	0.66	0.08	2.857	2.680	2.843	2 235	1.978	1.978		2.843	0.66	4.129	22.897	−0.416
	1956	129	12	0.05	—	0.05	—	2.580	—	2.580	1 268	1.921	1.921		1.574	0.08		27.026	−2.526
	1957	42	4	—	—		—				324	6.480	3.953						
1945	1948	889	6	0.66	—	0.66		1.347		1.347					1.347	0.66	1.197	0.673	−0.416
	1949	13 307	3 036	12.93	2.68	15.61	0.17	1.029	1.133	1.047					1.047	15.61	1.586	1.870	2.747
	1950	9 263	8 637	1.36	4.24	5.60	0.76	2.400	2.037	2.125					2.125	5.60	2.422	3.456	1.723
	1951	35 698	13 682	13.66	4.77	18.43	0.26	2.613	2.868	2.679	113	0.020	0.020		2.679	18.43	2.765	5.878	2.912
	1952	39 438	4 341	13.42	2.43	15.85	0.15	2.938	1.786	2.761	824	0.045	0.045		2.761	15.85	2.547	8.643	2.760
	1953	11 789	2 283	5.76	1.25	7.01	0.18	2.047	1.826	2.008	2 587	0.163	0.163		2.008	7.01	2.801	11.190	1.947
	1954	6 356	633	1.65	0.24	1.89	0.13	3.852	2.638	3.698	3 650	0.521	0.521		2.552	2.74	4.572	13.991	1.008
	1955	4 325	341	1.41	0.16	1.57	0.10	3.067	2.131	2.971	4 962	2.625	1.811		2.971	1.57	5.301	18.563	0.451
	1956	1 063	118	0.25	0.04	0.29	0.14	4.252	2.950	4.072	2 795	1.780	1.780		4.072	0.29	7.217	23.864	−1.238
	1957	389	41	0.08	0.01	0.09	0.11	4.862	4.100	4.777	810	2.793	2.793		4.777	0.09		31.081	−2.408
	1958	45									263	2.922	2.922						

(*Continued*)

APPENDIX TABLE A. The exploited life history of successive year-classes of Arcto-Norwegian cod. — (*Concluded*)

Year-class	Sample year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1946	1949	4 351	3	4.43	—	4.43		0.982		0.982				0.982	4.43	1.618	0.491	1.488
	1950	3 936	1 945	0.58	0.90	1.48	0.61	2.400	2.161	2.255				2.255	1.48	2.648	2.109	0.392
	1951	48 273	7 941	8.66	2.53	11.19	0.23	3.000	3.139	3.033	6	0.004	0.004	3.033	11.19	3.287	4.757	2.415
	1952	62 459	3 835	16.59	2.18	18.77	0.12	3.766	1.759	3.533	42	0.004	0.004	3.533	18.77	3.006	8.044	2.934
	1953	19 636	2 397	8.19	1.09	9.28	0.12	2.398	2.199	2.376	968	0.052	0.052	2.376	9.28	3.135	11.050	2.228
	1954	13 714	1 104	4.06	0.48	4.54	0.11	3.378	2.300	3.264	2 921	0.315	0.315	3.264	4.54	4.653	14.185	1.513
	1955	7 861	315	2.08	0.11	2.19	0.05	3.780	2.864	3.734	5 238	1.154	1.154	3.734	2.19	6.069	18.838	0.784
	1956	2 766	189	0.63	0.04	0.67	0.06	4.390	4.725	4.411	4 374	1.997	1.997	4.411	0.67	6.595	24.907	−0.400
	1957	1 451	116	0.38	0.01	0.39	0.03	3.819	11.600	4.018	1 595	2.381	2.381	4.018	0.39	5.946	31.502	−0.942
	1958	340		0.11	—	0.11	—	3.091		3.091	933	2.392	2.392	3.091	0.11		37.448	−2.207
	1959	76	3	—	—			3.800		3.800	191	1.736	1.736	3.800				
1947	1950	304	407		0.05	0.05	1.00		2.200	2.200				2.200	0.05	2.698	1.100	−2.996
	1951	54 032	6 580	1.42	2.06	3.48	0.59	3.200	3.194	3.197				3.197	3.48	3.161	3.798	1.247
	1952	85 563	11 596	12.08	6.71	18.79	0.36	3.900	1.728	3.126				3.126	18.79	2.830	6.959	2.934
	1953	44 830	9 209	17.23	4.41	21.64	0.20	2.600	2.089	2.496	360	0.019	0.019	2.496	21.64	2.823	9.789	3.073
	1954	31 985	2 907	10.43	1.34	11.77	0.11	3.067	2.169	2.964	2 007	0.093	0.093	2.964	11.77	3.919	12.612	2.468
	1955	23 192	1 244	5.88	0.45	6.33	0.07	3.945	2.764	3.862	5 953	0.506	0.506	3.862	6.33	5.477	16.531	1.845
	1956	5 465	764	1.22	0.19	1.41	0.13	4.480	4.021	4.418	8 459	1.337	1.337	4.418	1.41	6.788	22.008	0.344
	1957	2 484	487	0.58	0.05	0.63	0.08	4.282	9.740	4.714	3 133	2.222	2.222	4.714	0.63	7.198	28.796	−0.462
	1958	1 300	39	0.41	0.01	0.42	0.02	3.171	3.900	3.188	2 046	3.247	3.247	3.188	0.42	4.873	35.994	−0.867
	1959	172	91	0.09		0.09		1.911		1.911	976	2.324	2.324	1.911	0.09		40.867	−2.408
	1960	3	2								394	4.377	4.377					
1948	1951	24 543	1 379	0.04	0.39	0.43	0.91	3.400	3.536	3.524				3.524	0.43	3.079	1.762	−0.844
	1952	78 245	19 822	4.75	10.17	14.92	0.68	4.100	1.950	2.634				2.634	14.92	2.486	4.841	2.701
	1953	87 383	21 814	14.46	10.94	25.40	0.43	2.600	1.994	2.339				2.339	25.40	2.594	7.327	3.235
	1954	74 167	16 215	22.12	9.96	32.08	0.31	3.352	1.628	2.816	429	0.017	0.017	2.816	32.08	3.366	9.921	3.469
	1955	69 163	9 473	16.97	4.02	20.99	0.19	4.074	2.357	3.745	3 898	0.086	0.086	3.745	20.99	4.946	13.287	3.045
	1956	26 077	8 510	5.71	1.76	7.47	0.24	4.566	4.835	4.630	15 941	0.759	0.759	4.630	7.47	4.504	18.233	2.011
	1957	6 949	3 007	1.29	0.47	1.76	0.27	5.387	6.399	5.657	8 322	1.114	1.114	2.150	4.63	4.563	22.737	1.533
	1958	3 549	253	0.90	0.06	0.96	0.06	3.943	4.218	3.961	6.987	3.970	1.508	3.961	0.96	6.574	27.300	−0.041
	1959	1 096	232	0.29	0.04	0.33	0.12	3.779	5.800	4.024	2 478	2.582	2.582	4.024	0.33	8.235	33.874	−1.109
	1960	346	18	0.11	—	0.11	—	3.145	—	3.145	1 535	4.651	4.651	3.145	0.11	7.317	42.109	−2.207
	1961	244	41	0.14	—	0.14	—	1.636	—	1.636	542	4.927	4.927	1.636	0.14			
1949	1952	17 809	1 658	0.16	0.44	0.60	0.73	4.300	1.800	2.467				2.467	0.60	2.426	1.233	−0.511
	1953	100 082	6 538	2.12	3.02	5.14	0.59	2.700	2.165	2.386				2.386	5.14	2.704	3.659	1.637
	1954	118 507	12 365	19.35	7.18	26.53	0.27	3.500	1.722	3.019	8	0.002	0.002	3.019	26.53	3.720	6.363	3.277
	1955	144 162	16 557	28.99	7.47	36.46	0.20	4.974	2.217	4.408	177	0.007	0.007	4.408	36.46	4.733	10.083	3.597
	1956	66 212	14 994	13.80	2.88	16.68	0.17	4.800	5.206	4.870	3 419	0.094	0.094	4.870	16.68	4.937	14.816	2.815
	1957	26 649	8 932	6.54	1.26	7.80	0.16	4.075	7.089	4.562	3 692	0.221	0.221	4.562	7.80	3.764	19.753	2.054
	1958	6 823	879	1.54	0.22	1.76	0.13	4.431	3.995	4.377	5 260	0.674	0.674	1.619	4.76	3.678	23.517	1.560
	1959	2 852	700	1.01	0.13	1.14	0.11	2.824	5.384	3.116	6 236	3.563	1.311	3.116	1.14		27.195	0.131
	1960	661	13	—	—	—	—	—	—	—	3 466	3.040	3.040					
	1961	229	44	0.06	—	0.06	—	6.701	—	6.701	1 471	—	—	6.701	0.06			
	1962	—	151		—						307	5.118	5.118					
1950	1953	42 211	4 562	0.02	0.60	0.62	0.97	2.800	2.000	2.026				2.026	0.62	2.405	1.013	−0.478
	1954	126 472	11 050	5.42	5.55	10.97	0.51	3.600	1.991	2.784				2.784	10.97	3.120	3.418	2.397
	1955	164 145	37 332	11.71	17.05	28.76	0.59	5.300	2.191	3.457				3.457	28.76	4.179	6.538	3.360
	1956	170 904	66 744	23.25	14.72	37.97	0.39	4.900	4.665	4.809	1 311	0.046	0.046	4.809	37.97	5.159	10.717	3.637
	1957	48 409	30 839	9.68	5.24	14.92	0.36	5.001	5.884	5.311	3 751	0.099	0.099	5.311	14.92	5.190	15.876	2.701
	1958	21 412	5 830	5.48	1.28	6.73	0.14	3.929	4.555	4.048	7 606	0.510	0.510	4.048	6.73	5.970	21.066	1.907
	1959	8 [illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0.20	3.924	4.109	3.969	13 203	1.262	1.262	3.969	[illegible]	[illegible]	[illegible]	[illegible]
	1960	5 154	3 837	3.04	0.80	3.84	0.21	4.011	4.786	4.383	4 890	0.089	0.089	4.625	3.84	4.488	19.185	2.066
	1960	3 600	221	0.55	0.06	0.61	0.10	6.545	3.683	6.262	3 997	0.484	0.484	3.383	3.84	3.985	21.643	1.345
	1961	3 042	188	0.40	0.02	0.42	0.05	9.047	9.400	9.065	3 969	6.505	2.602	2.505	1.52	7.349	25.628	0.419
	1962	818	185	0.23	—	0.23	—	—	—	—	2 [illegible]	[illegible]	[illegible]	6.000	[illegible]	[illegible]	[illegible]	[illegible]

	1955	164 145	37 332	11.71	17.05	28.76	0.39	4.900	4.665	4.809	1 311	0.046	0.046	4.809	37.97	5.159	10.716	5.677		
	1956	170 904	66 744	23.25	14.72	37.97	0.39	4.900	5.884	5.311	3 751	0.099	0.099	5.311	14.92	5.190	15.876	2.701		
	1957	48 409	30 839	9.68	5.24	14.92	0.36	5.001	5.884	5.311	3 751	0.099	0.099	5.311	14.92	5.190	21.066	1.907		
	1958	21 412	5 830	5.45	1.28	6.73	0.14	3.929	4.555	4.048	7 606	0.510	0.510	4.048	6.73	5.970	27.036	0.974		
	1959	5 339	1 137	3.13	0.39	3.52	0.10	3.924	4.109	3.599	13 208	1.262	1.262	3.599	3.64	4.626	17.185	2.086		
	1960	9 134	3 237	3.95	0.80	4.75	0.21	3.911	4.795	3.383	3 899	0.484	0.484	3.383	3.84	4.488	21.643	1.345		
	1960	3 600	721	0.35	0.06	0.41	0.10	3.545	3.683	3.262	13 997	1.041	1.041	3.505	1.52	3.985	25.628	0.419		
	1961	3 042	188	0.40	0.02	0.42	0.05	9.047	9.400	9.065	3 969	6.505	2.602	6.990	0.53	7.349	32.977	−0.635		
	1962	818	185	0.22	0.02	0.24	0.08	3.718	9.250	4.197	2 033	4.841	3.486	4.179	0.24	9.070	42.047	−1.427		
	1963	136		0.02		0.02		6.800		6.800	686	2.859	2.859	6.800	0.02	8.348	50.395	−3.912		
1952	1955	3 692	316		0.10	0.10	1.00	6.100	2.200	2.200				2.200	0.10	2.642	1.100	−2.302		
	1956	21 127	2 307	0.51	0.27	0.78	0.35	5.100	5.000	5.065				5.065	0.78	5.156	3.742	−0.248		
	1957	16 795	8 734	3.39	1.32	4.71	0.28	4.955	6.000	5.247				5.247	4.71	4.716	8.898	1.550		
	1958	31 064	9 951	8.19	1.71	9.90	0.17	3.793	5.819	4.142	105	0.022	0.022	4.142	9.90	3.709	13.614	2.293		
	1959	13 173	2 997	4.57	0.54	5.11	0.11	2.882	5.550	3.164	557	0.056	0.056	3.164	5.11	4.744	17.323	1.631		
	1960	7 110	294	1.21	0.06	1.27	0.05	5.876	4.900	5.830	1 263	0.247	0.247	5.830	1.27	6.913	22.067	0.239		
	1961	3 619	295	0.85	0.05	0.90	0.06	4.256	5.900	4.347	2 318	1.825	1.825	4.347	0.90	7.255	28.980	−0.105		
	1962	642	271	0.15	0.01	0.16	0.06	4.280	27.100	5.706	2 006	2.229	2.229	5.706	0.16	10.778	36.235	−1.833		
	1963	657		0.08		0.08		8.212		8.212	611	3.819	3.819	8.212	0.08		47.013	−2.526		
1953	1956	10 430	146	0.02		0.02		5.200	5.000	5.200				5.200	0.02	5.201	2.600	−3.912		
	1957	20 852	5 977	1.98	0.75	2.73	0.27	4.900	6.000	5.202				5.202	2.73	4.961	7.801	1.004		
	1958	42 735	22 462	9.83	3.98	13.81	0.29	4.346	5.645	4.720				4.720	13.81	4.095	12.762	2.625		
	1959	37 941	10 070	12.43	1.62	14.05	0.12	3.054	6.216	3.419	363	0.026	0.026	3.419	14.05	4.363	16.857	2.639		
	1960	21 805	2 260	3.91	0.75	4.66	0.16	5.578	3.013	5.165	995	0.071	0.071	5.165	4.66	5.378	21.220	1.539		
	1961	12 374	1 617	3.04	0.24	3.28	0.07	4.070	6.738	4.266	3 090	0.663	0.663	4.266	3.28	6.046	26.598	1.188		
	1962	4 403	766	0.95	0.08	1.03	0.08	4.636	9.575	5.020	4 601	1.403	1.403	5.020	1.03	7.802	32.644	0.030		
	1963	1 135	129	0.16	0.01	0.17	0.06	7.094	12.900	7.435	1 622	1.575	1.575	7.435	0.17		40.446	−1.772		
1954	1957	6 110	7 595	0.08	0.06	0.14	0.43	5.000	6.000	5.429				5.429	0.14	5.286	2.714	−1.966		
	1958	48 585	77 030	4.38	7.11	11.49	0.62	4.400	5.600	5.143				5.143	11.49	4.846	8.000	2.442		
	1959	59 197	69 004	14.84	8.90	23.74	0.37	3.200	6.800	4.549				4.549	23.74	4.383	12.846	3.167		
	1960	57 119	18 465	13.06	5.23	18.29	0.29	4.375	3.531	4.135	972	0.041	0.041	4.135	18.29	4.249	17.229	2.907		
	1961	23 432	10 511	5.61	2.68	8.29	0.32	4.178	3.922	4.094	2 467	0.135	0.135	4.094	8.29	5.472	21.478	2.115		
	1962	12 141	5 538	2.38	0.86	3.24	0.27	5.102	6.441	5.457	5 779	0.697	0.697	5.457	3.24	7.516	26.950	1.176		
	1963	3 157	579	0.45	0.15	0.60	0.25	7.015	3.860	6.227	5 424	1.674	1.674	6.227	0.60		34.466	−0.511		
1955	1958	15 277	14 291	0.55	0.34	0.89	0.38	4.500	5.600	4.920				4.920	0.89	4.950	2.461	−0.117		
	1959	30 051	35 788	5.33	3.55	8.88	0.40	3.300	7.500	4.978				4.978	8.88	4.420	7.411	2.184		
	1960	56 535	13 701	14.38	3.81	18.19	0.21	3.929	3.597	3.860				3.860	18.19	4.077	11.831	2.901		
	1961	32 537	15 117	8.75	2.52	11.27	0.22	3.719	5.998	4.229	571	0.031	0.031	4.229	11.27	4.601	15.908	2.422		
	1962	19 938	7 553	4.80	1.20	6.00	0.20	4.153	6.294	4.582	2 214	0.196	0.196	4.582	6.00	5.755	20.509	1.792		
	1963	8 112	1 407	1.42	0.28	1.70	0.16	5.712	5.024	5.598	3 990	0.665	0.665	5.598	1.70		26.264	0.531		
1956	1959	10 328	15 719	0.50	1.03	1.53	0.67	3.400	8.200	6.631				6.631	1.53	5.531	3.315	0.425		
	1960	79 100	15 825	16.75	4.67	21.42	0.22	4.722	3.388	4.432				4.432	21.42	4.561	8.846	3.063		
	1961	73 854	46 055	14.88	7.66	22.54	0.34	4.000	6.010	4.684	93	0.004	0.004	4.684	22.54	4.654	13.407	3.114		
	1962	64 364	24 477	14.76	4.71	19.47	0.24	4.357	5.196	4.560	745	0.033	0.033	4.560	19.47	4.883	18.061	2.970		
	1963	23 396	4 956	4.56	1.21	5.77	0.21	5.131	4.096	4.914	2 839	0.146	0.146	4.914	5.77		22.944	1.753		
1957	1960	27 949	2 202	3.80	0.60	4.40	0.14	5.000	3.670	4.819				4.819	4.40	4.733	2.409	1.482		
	1961	88 144	49 289	10.60	4.96	15.56	0.32	4.000	6.000	4.638	20	0.005	0.005	4.638	15.56	4.746	7.142	2.745		
	1962	120 746	35 837	21.20	6.77	27.97	0.24	4.700	5.293	4.843	94	0.006	0.006	4.843	27.97	4.812	11.888	3.320		
	1963	67 383	13 632	13.75	3.34	17.09	0.20	4.899	4.081	4.740	598	0.021	0.021	4.740	17.09		16.700	2.839		
1958	1961	46 667	17 220	1.69	0.54	2.23	0.24	4.000	6.000	4.484				4.484	2.23	4.692	2.242	0.802		
	1962	133 685	26 570	12.17	4.07	16.24	0.25	4.800	5.200	4.901				4.901	16.24	4.830	6.934	2.787		
	1963	157 346	22 725	24.74	6.03	30.77	0.20	5.000	3.768	4.759				4.759	30.77		11.764	3.428		
1959	1962	48 233	6 298	1.13	0.20	1.33	0.15	4.900	5.200	4.945				4.945	1.33	4.877	2.472	0.285		
	1963	99 563	9 497	8.64	1.65	10.29	0.16	5.000	3.800	4.810				4.810	10.29		7.349	2.332		
1960	1963	17 084	1 829	0.47	0.03	0.50	0.06	5.000	3.800	4.928				4.928	0.50		2.464	−0.693		

APPENDIX TABLE B. Comparison of USSR and English catch per unit effort data for the Barents Sea cod fishery.

Age	Calendar year																	
	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
	USSR Numbers/1 hr fishing																	
6	48.21	70.30	93.14	113.99	60.40	79.35	116.64	82.34	151.02	251.42	233.36	58.68	35.32	53.74	55.09	30.69	60.45	71.70
7	35.12	55.82	131.24	117.53	89.40	47.86	68.10	26.38	58.35	94.80	81.44	56.58	25.66	17.35	21.79	18.98	17.91	23.04
8	30.01	14.81	31.75	41.19	46.81	20.78	16.44	15.19	22.31	36.27	27.73	35.63	28.49	10.91	8.71	10.30	9.05	7.55
9	61.93	17.57	20.04	15.63	20.54	7.56	7.83	4.00	8.58	12.37	5.78	6.55	8.95	7.56	3.11	2.99	3.86	2.75
10	45.02	25.84	5.65	4.26	9.36	2.52	2.35	1.60	5.15	6.60	2.89	3.14	5.18	3.64	1.87	1.47	0.60	1.02
11	13.41	27.22	10.23	6.75	6.34	1.89	1.56	0.80	2.57	2.47	1.16	2.10	2.12	1.12	0.93	0.21	0.35	0.61
12	3.51	5.86	3.88	3.91	1.81		0.78	0.80				0.52	0.47	0.28	0.31	0.23	0.49	0.17
13	1.28	3.79	1.77	2.13	1.21											0.21		0.11
14	0.63	2.07	2.11	1.06	0.61											0.27		0.26
15	1.28				0.30													0.05
	English Numbers/100 ton-hours — See Appendix Table A.																	
	Ratio USSR/English																	
6	3.7	3.1	3.8	3.4	9.2	5.8	7.1	4.8	6.8	8.6	10.1	6.0	4.3	4.4	4.2	3.5	4.1	5.2
7	3.7	3.1	3.8	5.8	5.9	4.2	5.1	3.2	5.6	5.6	5.9	6.0	4.5	3.9	5.6	3.4	3.7	5.0
8	3.7	3.1	3.8	4.5	4.2	3.1	3.9	2.7	5.6	6.1	4.9	5.4	5.3	3.6	7.3	3.3	3.9	5.4
9	3.7	3.1	3.8	2.3	4.1	1.8	3.7	2.4	3.7	5.9	4.8	1.9	2.1	3.6	2.2	3.3	4.3	6.9
10	3.7	3.1	3.8	1.5	4.7	1.5	1.5	1.1	5.1	4.7	4.8	5.2	5.8	3.6	1.7	2.9	3.0	5.0
11	3.7	3.1	3.8	4.2	5.3	3.1	1.7	2.0	3.9	3.5	3.9	5.2	5.3	3.7	2.3	1.0	1.7	6.1
12	3.7	3.1	3.8	2.8	6.0		3.9	4.0				5.2	4.7	2.8	3.1	2.3	4.9	—
13		3.1	3.8	2.7	1.5													
14			3.8	1.8	3.0													
15					1.5													
Mean ratio:	3.7	3.1	3.8	3.2	4.5	3.3	3.8	2.9	5.1	5.7	5.7	5.0	4.6	3.7	3.8	2.8	3.7	5.6

Factors Affecting the Response of Trout to an Electric Field in Fresh and Salt Water[1]

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ABSTRACT

The "minimum response" level of *Salmo trutta* to an alternating current field increased with angle to the field, temperature, resistivity, and fatigue, with a wide range of individual variation. The drop in potential across the length of a fish ("body-voltage") varies directly with length and is not a constant for the species in either fresh or salt water. Embryo trout show a fully developed response 2 weeks after hatching.

INTRODUCTION

Herman (1885) found that freshwater fish and tadpoles in a direct current (D.C.) field of suitable intensity arranged themselves parallel to the line of current, facing the anode, and moved towards it. This response, and the narcosis produced by both D.C. and alternating current (A.C.) fields at higher voltages, have had economic applications in fresh water in catching fish (e.g. Haskell, 1950) and directing them past hydroelectric turbines (e.g. Lethlean, 1953).

MacMillan (1928) showed that the voltage gradient required for narcosis varied inversely with the length of the fish. This result, based on a mixed group of salmonids in fresh water, was extended to three species of cyprinids by Holzer (1931) and expressed as the "law of constant body-voltage," which states that the nose-to-tail voltage required for a given reaction is a constant for any species, irrespective of the length of individual fish.

Bary (1956) investigated the effect of pulsed D.C. (the most promising method economically in sea water) on a group of mullet (*Mugil auratus*) and found that Holzers' law did not hold in sea water although its application had been assumed theoretically by Holzer (1931), Kreutzer (1950), and Meyer (1952). Bary suggested that "A series of parallel experiments in both seawater and freshwater would show to what degree the differences may be reconciled, or whether they are fundamental to the requirements of fish in the two media. Clarification is desirable as McMillan's and Holzer's findings have formed much of the basis of present-day thought on the effects of electric fields on fish."

The main aim of the present work was to follow up this suggestion by comparing the reactions of trout (*Salmo trutta*) in fresh water and sea water.

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Trout seemed ideal as they are readily available in a wide range of sizes and can be acclimatized to sea water successfully. In the course of the work the effect of several variables on the level of response was measured to investigate potential sources of error, and these results are outlined. In addition, trout embryos were tested to find out at what age the typical response is first shown.

MATERIAL AND METHODS

Trout eggs and 1-, 2-, and 3-year-old fish were bought from the Howietown Hatcheries, Stirling. These gave a size range up to 30 cm and were supplemented by a few 15–25 cm trout from the Carron River, Kincardineshire. A few larger fish (30–60 cm) were obtained from one of the Brown Trout Research Laboratory's tagging stations on a tributary of the Dee, Aberdeenshire. These were mostly sea-trout, the migratory form of *S. trutta*, but all had spawned and so were judged to have been in fresh water for at least a month. The fish were kept in two large tanks with constant running water 6 inches deep. Brick drainpipes were provided for shelter.

A 60 × 8 × 8 inch tank was made of teak 1-inch thick, and sealed with aquarium cement. The electrodes consisted of eight $\frac{3}{8}$-inch diameter carbon rods supported in a brass connecting bar, and were placed 1 m apart. The power supply was taken from the laboratory 240 v, 50 cycle A.C. mains, passed through a resistance transformer from which 20, 30, or 90 v could be tapped. Embryos required up to 80 v/m (90 v supply with 25,000 ohm rheostat) and larger trout 2–5 v/m (30 v supply with 25,000 ohm rheostat) or 5–12 v/m (30 v supply with 25,000 and 1000 ohm rheostats in parallel). In sea water only the 1000-ohm rheostat was required, with 90 v for embryos and 20 v for all larger fish. The electric field was checked for uniformity with a voltmeter, the only irregularities found being a 5% increase close to the electrodes and in the corners of the tank, but these did not affect the central part used in the experiments.

To facilitate taking voltage readings while watching for the fish's response, mirrors were arranged to provide an image of the fish just above the voltmeter needle.

Before use the experimental tank was emptied and washed to remove slime and dust, and the electrodes cleaned if necessary. The tank was then refilled to a standard depth of 20 cm, and the resistance and temperature of the water noted. Trout from the storage tank were caught with minimal disturbance by up-ending their drainpipe shelters into a soft cloth net. The fish were kept central and aligned to the electric field by perspex cages of the type used by Bary (1956). Fish longer than 40 cm were held in a sleeve of netting, and a small paper groove was used for embryos. They were allowed 5 min to settle down after being placed in the restraining cage.

The voltage between the electrodes was gradually increased over about 30 sec by adjusting the rheostats until the "minimum response" jerk described below occurred when the current was turned down. This was repeated six

times to compensate for small variations in alignment to the electric field, allowing a minute for recovery between responses.

The "Minimum Response" Reaction

As the voltage increases, the trout may make some slight, uneasy movements. Then the pectoral fins are spread wide and held forwards just before the characteristic jerk or "minimum response," which is caused by a powerful twitch of the tail. Occasionally two or three jerks may be given in quick succession. If the voltage is further increased the fish twists and presses against the sides of the restraining cage more and more wildly until paralysis sets in, when it becomes rigid except for slight gill and fin movements. Balance is lost and the fish may turn upside down.

The fundamental nature of the response was indicated by experiments on a trout which died of a gill injury. After it was "dead" 20 min, in the common usage of the term, the normal "minimum response" could be elicited; and 2 hr later, after rigor had set in over most of the body, the characteristic spreading of the pectoral fins occurred at the normal voltage, although no jerk followed. Vibert (1963) attributes the various responses of a fish in a D.C. field to stimulation of the appropriate motro and sensory nerves, culminating in tetany when the muscle fibres are stimulated directly.

The two most commonly used end-points in measuring the response of fish to electric fields are the "minimum response" and narcosis level. As the relation between these is constant (Holzer, 1931; Lethlean, 1953; Bary, 1956), and narcosis may have harmful effects (Hauck, 1949; Taylor et al., 1957), only the "minimum response" was used in the present study.

RESULTS

1. Factors Affecting the "Minimum Response"

Preliminary tests were made on a few fish in fresh water to examine possible sources of error due to variations in temperature, resistivity, alignment in the field, fatigue, and other factors. Figures 1–3 show, for simplicity, results from single fish, the plotted points being the mean of six responses. The effect of each variable, however, was noted over at least part of its range in several fish, and the results shown appeared quite typical.

Alignment in Field

A trout in a restraining cage was aligned at various angles to the electric field, and the voltages required for "minimum response" are shown in Fig. 1. At angles of less than 30° to the field the error is slight, but the mean of six responses was always taken to reduce this effect as much as possible.

Temperature

After initial cooling with ice, the temperature in the experimental tank was gradually raised by adding hot water, and a series of "minimum response" readings taken (Fig. 2). The fish was allowed 5 min to acclimatize to each

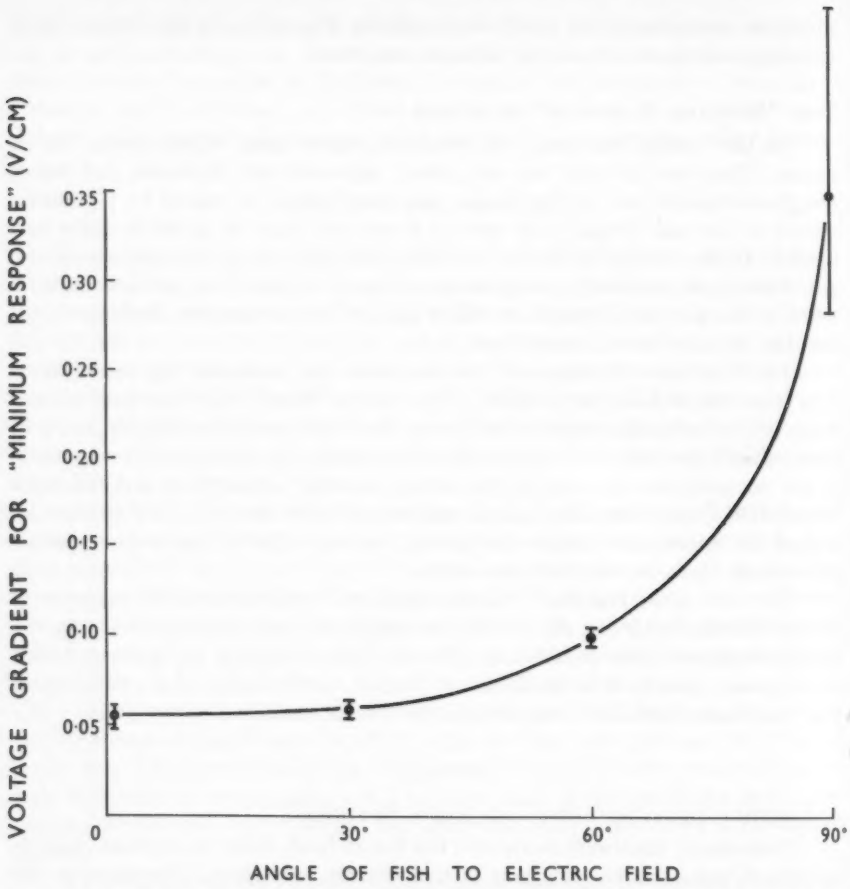

FIG. 1. Variation in "minimum response" level with the angle of the fish to the electric field. Curve fitted by eye and range of six responses indicated by vertical lines.

temperature, and the results shown have been corrected for changes in resistivity with temperature using the data in Fig. 3. The decreasing sensitivity to an A.C. field at increasing temperatures conflicts with the results of Bary (1956) who found no significant difference in mullet over the range of 8–20 C; and of Lethlean (1953) who found that trout required higher voltages to produce stimulation and paralysis at lower temperatures over the range 35–70 F. The difference may be due to the type of current used, as Lamarque (1965) found that with a reduction in temperature the effect of pulsed current decreased, but that of continuous current increased. These results merit further investigation, but the variation was too small over the range of temperatures encountered (5–10 C) to affect the present experiment.

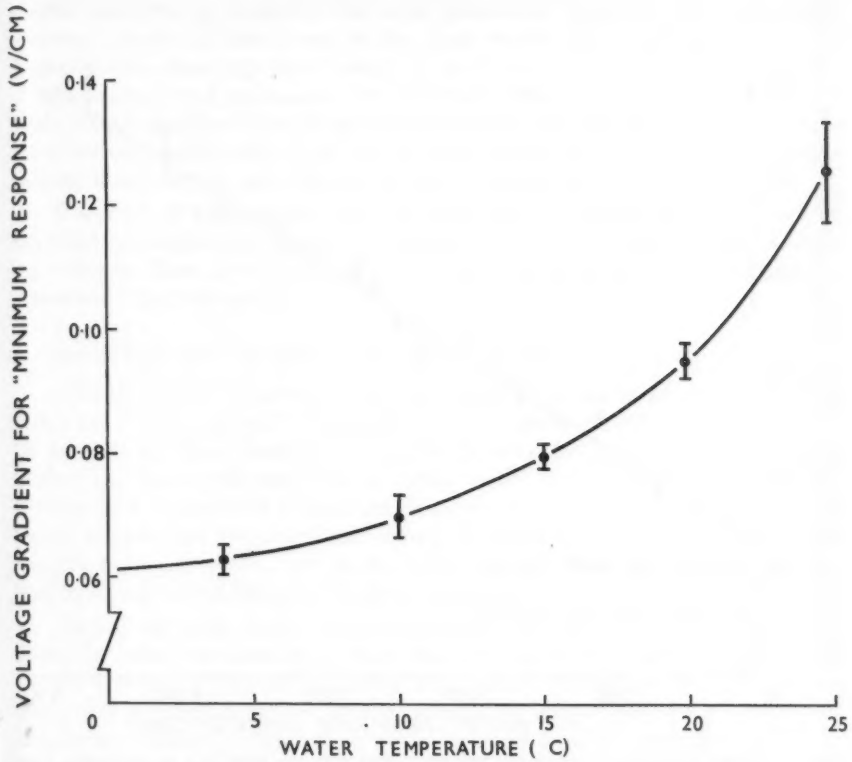

FIG. 2. Variation in "minimum response" level with water temperature, with concurrent changes in resistivity corrected to 5600 ohms/cm cube. Curve fitted by eye, and range of six responses indicated by vertical lines.

RESISTIVITY

Various resistivities were obtained by adding increasing quantities of sea water, the trout being allowed 5 min to acclimatize to the next salinity before the "minimum response" was noted. The response level varied directly with resistivity (Fig. 3). As the tap water used in the main experiment varied in resistivity from 4000 to 6000 ohms per cm cube, a correction factor based on Fig. 3 was applied to all but a few early results which are subject to an error of up to 15%. Fortunately, even this error is slight compared with the effect of individual variation discussed below.

FATIGUE

The fish were disturbed as little as possible, and the experimental procedure standardized so that all fish would be similarly affected. Some large fish struggled considerably during handling, however, so the effect of fatigue was investigated

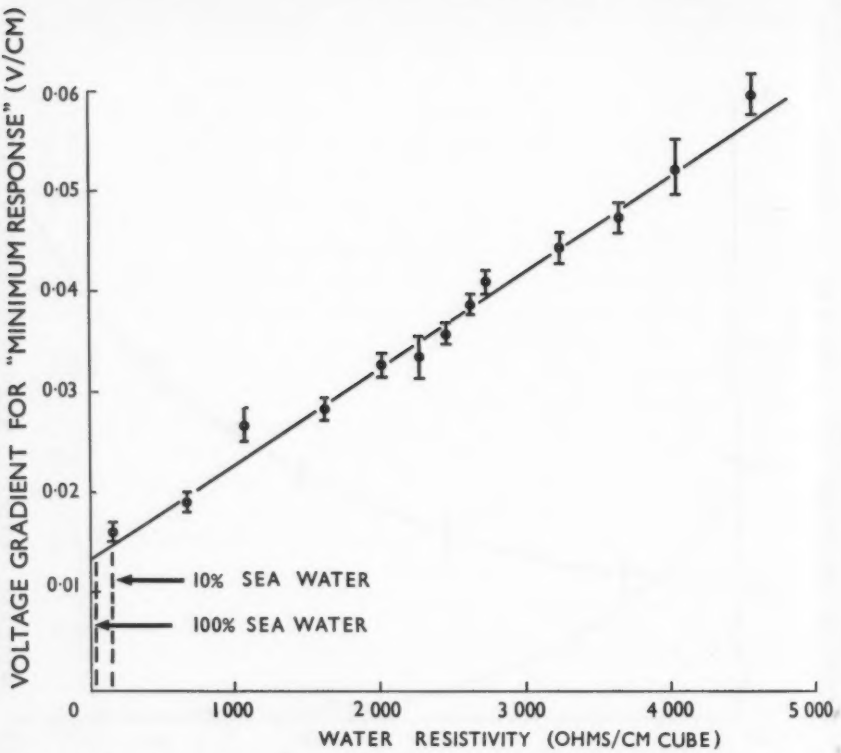

FIG. 3. Linear variation in "minimum response" level with the resistivity of the water. Line fitted by eye, and range of six responses indicated by vertical lines. Note the insignificant difference in response expected in 10% and 100% sea water.

to see if a correction factor was necessary. The "minimum response" level increased by only 10% for a fish which had been chased round a tank for 20 min without rest, until it lay exhausted on its side. Consequently, the normal 1–2 min handling would have had no significant effect.

ANAESTHESIA

The largest trout proved too difficult to handle and their "minimum response" was recorded after they were anaesthetized in a 0.5% solution of urethane at about 10 C until quite relaxed, although still moving the gills. This took from 3 to 8 min. Seven fish showed an average rise in "minimum response" level of 2% (maximum 7%) which is of no consequence.

INDIVIDUAL VARIATION

Although other workers have given little more than passing attention to individual variation, it is clear from the otherwise unexplained scatter in their

results that this is normally the most important variable. The "minimum response" levels of three trout of the same length (19.3–19.5 cm) and shape illustrate this. Readings were taken for each fish under the same conditions of temperature and resistance, five times on different days over 2 weeks and again after 4 months. The range extremes of the response level for each fish in volts per centimeter were 0.027–0.0 9, 0.050–0.064, and 0.081–0.092, showing that each fish had its own distinct level of stimulation.

Three of 80 trout tested did not show the "minimum response" jerk at any time, although they appeared normal in every other respect. Under increasing voltages these individuals merely became steadily wilder in their movements until narcosis set in.

2. "Body-Voltage" in Fresh and Salt Water

The change in potential along the length of a fish in an electric field is called the "body-voltage." In practice it is not measured directly but obtained by multiplying the voltage per centimeter between the electrodes by the length of the fish. Since fresh water has a higher resistivity than that of a trout, the electric field is distorted around the fish and the actual voltage drop along its length is less than the calculated value. Fortunately, trout of all sizes have roughly the same shape, and at any given resistivity of the medium the distortion should affect fish of all lengths similarly.

Due to the wide scatter caused by individual variation, little is gained by using the same fish more often than once, and as many trout as possible were tested. Unfortunately, acclimatizing trout to sea water proved difficult, and many died at salinities of over 70% sea water. The longest period a trout survived in pure sea water was just over a week. As no change in "minimum response" correlated with length of time in salt water was found, results from fish acclimatized for only a few minutes were considered valid. In addition, since the "minimum response" varies linearly with resistivity, there is no significant difference in the response level in 10% and 100% sea water (see Fig. 3). Consequently, it was unnecessary to risk acclimatizing the trout to concentrations of over 10% sea water.

Figure 4 compares the "body-voltage" of 71 trout of various lengths in fresh water and 32 trout in salt water. Clearly, a relatively higher voltage is required for the "minimum response" of larger fish in both fresh and salt water. Thus the "body-voltage" is not constant for any given species regardless of length as maintained by Holzer (1931), but varies directly with length both in sea water, as Bary (1956) found, and in fresh water.

3. "Minimum Response" of Trout Embryos

Trout ova were reared in constant running water at 7–13 C, and the date of hatching was taken as the day on which most hatched. Five embryos were used in each test, six responses from each being averaged as for the larger fish. The results are summarized in the following table.

Age of embryo	Mean length (*cm*)	"Minimum response" level (*v/cm*)
2 weeks pre-hatching	1.3	No response
Newly hatched	1.6	" "
1 week after hatching	1.8	1.2–0.4
2 weeks " "	2.0	0.65
6 weeks " "	2.4	0.55
10 weeks" "	2.5	0.38

Prior to 1 week after hatching, embryos gave no clear "minimum response" jerk but became violent at fields of 0.8–0.9 v/cm. The five embryos tested 1

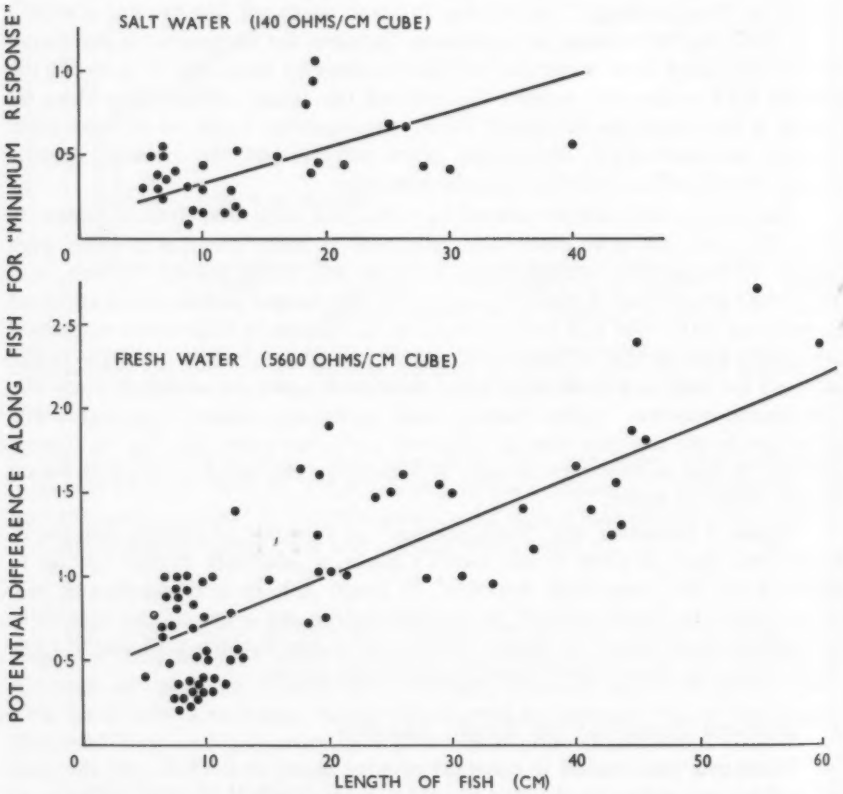

FIG. 4. Potential difference along the length of a trout ("body-voltage") required for "minimum response." Each point is the mean of six responses of one fish, and the lines are the regressions of y on x. "Body -voltage" increases with length for trout in both salt and fresh water.

week after hatching behaved curiously: two merely became violent at 0.8–0.9 v/cm, but the other three gave a true "minimum response" jerk. The voltage necessary fell with each stimulation, however, which never happened with any other trout. For example, one embryo gave consecutive responses at 1.2, 1.0, 0.9, 0.6, 0.5, and 0.5 v/cm. Two weeks after hatching, nearly all embryos showed a clear "minimum response" with an average range of variation of $\pm 7\%$ which is comparable with the $\pm 6\%$ found in large fish. The actual response value, however, was still relatively high and did not fall in line with that for large trout until about 10 weeks after hatching, when feeding started.

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NOTES

A Bacterial-Toxin Type of Phospholipase (Lecithinase C) in a Marine Phytoplanktonic Chrysomonad

Although the phospholipids of unicellular and planktonic algae have been fairly extensively investigated (see Kates and Volcani, 1966, and references cited therein), there is very scanty information on the enzymes involved in their metabolism. In particular, phospholipid hydrolysis appears to have been overlooked by previous workers. The availability of algal material from 13 species of marine phytoplankters (representing six classes of algae) has offered us the opportunity to survey these organisms for the occurrence of lecithinase activity by using a radioactive tracer method for the simultaneous determination of the various lecithin hydrolyzing enzymes (resulting in formation of glyceryl-phosphorylcholine, phosphorylcholine, and free choline). Our preliminary studies have revealed the occurrence of a potent lecithinase C[1] (reminiscent of certain bacterial toxins involved in food poisoning) in the chrysomonad *Monochrysis lutheri*. However, the other phytoplankters examined gave no indication of any significant lecithinase activity.

The following algal species were examined; they are listed under the class to which they are known to belong.

Bacillariophyceae:	*Cyclotella nana; Phaeodactylum tricornutum*; *Skeletonema costatum.*
Chlorophyceae:	*Dunaliella tertiolecta*; *Tetraselmis maculata.*
Chrysophyceae:	*Isochrysis galbana*; *Monochrysis lutheri.*
Cryptophyceae:	*Cryptomonas* sp. (3 C); *Hemiselmis virescens*; *Rhodomonas lens.*
Dinophyceae:	*Amphidinium carteri.*
Myxophyceae:	*Agmenellum quadruplicatum*; *Anacystis marina.*

The algae were grown photoautotrophically in axenic mass culture and cells were harvested towards the end of (or soon after) exponential growth by methods described elsewhere (Antia and Kalmakoff, MS, 1965). Acetone powders were prepared from the algal cells as previously described (Antia and Watt, 1965) and were used for the lecithinase tests.

The radioactive tracer method developed by Bilinski and Jonas (1966) was used for assay of lecithinase activity. The lecithin employed as substrate was labeled in vivo with choline-methyl-^{14}C using live trout as described by

[1]The system of nomenclature recommended by the International Union of Biochemistry (Florkin and Stotz, 1964) is followed in this paper, according to which phospholipases C and D produce phosphorylcholine and choline, respectively, from hydrolysis of lecithin.

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these authors, and it was isolated by aluminum oxide and silicic acid chromatography according to the procedure of Saito and Hanahan (1962). The incubation conditions are described in Table I.

The lecithinase assays on the algal acetone powders revealed a very high level of activity in *Monochrysis lutheri* in contrast to all the other species which did not show any significant activity. The experiments conducted with *M. lutheri* are summarized in Table I. The hydrolysis of lecithin resulted in negligible conversion to free choline and glycerylphosphorylcholine. The principal labeled product of hydrolysis was in the form of bound choline, resistant to mild acid hydrolysis (1 N HCl, 100 C, 20 min) but releasing choline only after stronger hydrolytic treatment (2 N HCl, 125 C, ca. 50% hydrolysis after 5 hr), which properties indicate the presence of phosphorylcholine. The high level of this type of lecithinase activity in *M. lutheri* was found to occur in each of two separately grown cultures of the organism. That the acetone powder from one of these cultures (*B* in Table 1) has shown such high activity after nearly 2 years of storage (in evacuated container at −30 C) suggests that the enzyme may be very stable under these conditions.

TABLE I. Lecithinase activity of *Monochrysis lutheri* and spinach leaves.

Acetone powder	Incubation conditions[a]		Products of hydrolysis		
	Protein nitrogen (*mg*)	Duration (*min*)	Free choline	Glyceryl phosphoryl choline	Phosphoryl choline
			% conversion[b]		
M. lutheri: culture *A*	1.94	120	<1	Traces	100
" "	1.94	120	<1	Nil	84
" "	0.97	120	<2	"	100
" "	0.97	120	<1	"	100
M. lutheri: culture *B*	2.00	120	<2	"	70
" "	2.00	120	<1	Traces	100
" "	1.00	40	<2	"	100
" "	1.00	40	<2	Nil	98
" "	1.00	20	<2	"	70
" "	1.00	20	<2	"	100
" "	0.40	20	<1	"	46
Spinach leaves	1.30	120	8.1 ±0.88 (6)[c]	"	4.0 ±0.91 (6)[c]

[a]Incubation temperature, 35 C; total volume, 1.0 ml; incubation medium, NaK phosphate buffer 0.1 M, *p*H 7.0; substrate, 0.5 mg lecithin-^{14}C with the following composition: 3.5% P; 13.5% choline; 17,500 cpm per milligram.

[b]Expressed as per cent of total radioactivity of the substrate.

[c]Mean value and standard deviation. The number of experiments is indicated in parentheses.

The formation of phosphorylcholine from the activity of *M. lutheri* was confirmed chromatographically as follows. After a 120-min incubation period (Table I), the water-soluble products of hydrolysis were examined by paper chromatography with the following solvent systems: ethanol – concentrated ammonia – water (90:5:5, v/v); *n*-propanol – concentrated ammonia – water (60:30:10, v/v) (Bilinski and Jonas, 1966). In both solvent systems, over 95% of the radioactivity was recovered at the R_F zones corresponding to a phosphorylcholine standard. Two ways are known by which phosphorylcholine may be formed enzymically: the action of lecithinase C on lecithin, and the direct phosphorylation of choline by adenosine triphosphate catalysed by choline phosphokinase (Dawson, 1955). It seems unlikely that, under the conditions used, appreciable quantities of phosphorylcholine could be formed through the activity of the latter enzyme.

Although phospholipase C is known to be produced by several strains of bacteria and by higher plants (see review of Kates, 1960), the powerful and almost exclusive nature of this type of lecithinase activity observed in *M. lutheri* recalls similar activity associated with the toxins of *Clostridium perfringens*, *Bacillus cereus*, and other bacteria involved in food poisoning (Nygren, 1962). This observation may have important implications in the food-chain associated with blooms of *M. lutheri* in the marine environment, although no cases of mass mortality at the upper trophic levels ensuing from this chrysomonad have yet been reported. Further work is planned to characterize the phospholipase C of *M. lutheri* and to test the expected toxigenicity of this organism to possible predators.

Our failure to detect any significant lecithinase activity in the other phytoplankters examined was surprising, since our assay procedure was found satisfactorily applicable to preparations from spinach leaves. As shown in Table I, the leaf acetone powder displayed the types of phospholipase activity known to occur in spinach (Kates, 1955). Further, the acetone powder showed considerably greater concentration of activity than an equivalent freshly prepared leaf homogenate. Since most green algae and diatoms contain lecithin (Kates and Volcani, 1966), it seems likely that they should have lecithinase activity and our inability to detect such activity in the members of these groups may be due to sub-optimal assay conditions. Recently, Nichols et al. (1965) found that lecithin and phosphatidylethanolamine are absent from the lipids of the blue-green algae they examined. This may account for our inability to detect lecithinase activity in the species belonging to the Myxophyceae, although their lipid composition has not yet been determined.

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A Preliminary Communication on the Biological Activity of 1α-Hydroxycorticosterone Isolated from Cartilaginous Fish

Recently, a new steroid, 1α-hydroxycorticosterone (1α-OH B), was isolated from the blood and interrenal incubates of two species of skate (Idler and Truscott, 1966a). Since 1α-OH B is the principal corticoid thus far detected in the plasma of these animals, it might be expected to show biological activity.

We now wish to report that the steroid is a potent mineralocorticoid for the rat. It apparently lacks glucocorticoid activity since it failed to promote the deposition of liver glycogen in the adrenalectomized mouse.

The procedures for preparation and purification of materials are reported elsewhere (Idler and Truscott, 1966a, b, c).

The mineralocorticoid activity of 1α-OH B was compared with that of 11-deoxycorticosterone (DOC). Male rats were adrenalectomized 48 hr before the injection of a sodium chloride load. Steroids were administered subcutaneously when the salt load was given and again after 3 hr. The urethras were ligated 4 hr after the salt load and urine was collected from the 4th to the 6th hr. Urinary sodium and potassium were determined using a flame spectrophotometer.

Sodium and potassium excretion, after 1α-OH B administration, was determined at four levels of steroid and for the control group. Sodium retention and potassium excretion were observed with DOC and 1α-OH B. The sodium retaining efficacy of DOC was proportional to the dose in the range 1.5 – 6.0 μg and was significantly different from the control ($P < 0.01$). There was a linear response to 1α-OH B for sodium retention in the same range which was also significantly different from the control ($P < 0.02$). Under the conditions of the bioassay, 1α-OH B was 70% as active as DOC in promoting the retention of sodium.

In a liver glycogen deposition bioassay for glucocorticoids following the procedure of Venning et al. (1946), no significant rise of liver glycogen resulted from the administration of 11, 22, or 44 μg of 1α-OH B to adrenalectomized mice. By contrast, 10, 20, 40, and 50 μg levels of standard cortisone evoked very significant responses.

It is difficult to predict biological activities for steroids entirely on the basis of functional groups because absorption, metabolism, excretion, and other factors must be considered but cannot yet be accurately predicted (Sarett et al., 1963). In the cortisol series a wide variety of hydroxylations have generally diminished biological activity, a notable exception being the 16α-OH group (Fried and Borman, 1958; Sarett et al., 1963). Therefore, it is of particular interest that the 1α-OH group converted corticosterone, a corticoid that possesses only minimum effects on electrolyte balance (Dorfman, 1962), to a potent

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mineralocorticoid. There are few steroids with which to compare 1α-OH B. The 1ξ-OH group introduced on 9α-fluorocortisol by *Rhizoctonia ferrugena* has been reported to diminish mineralocorticoid activity (McAleer et al., 1958). However, this 1-OH group is probably the β-epimer (Nussbaum et al., 1959; Bolt et al., 1965), although Schwarz et al. (1964) reasoned, on theoretical grounds, that it is the α-epimer. We were unable to detect 1α-hydroxylation of corticosterone by *R. ferrugena* (unpublished information). There are instances when a steroid is more potent for the species in which it occurs, and attempts to assess biological activity of 1α-OH B in skate are in progress.

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Atlantic wolffish (*Anarhichas lupus* L.) eggs off southern Nova Scotia

In waters off eastern North America wolffish are common from Davis Strait to Cape Cod (Leim and Scott, 1966). Though some studies have been made of the same species in European waters, the life history of the American species has received little attention. They lay clusters of large eggs on bottom (as in European waters). Larvae have been taken fairly commonly (usually just off bottom) in the Gulf of Maine (Bigelow and Schroeder, 1953). The occurrence of eggs in eastern North American waters has been reported only once before. McKenzie and Homans (1937) reported a single cluster of about one quart (1.3 liter) in volume which had been dragged up near Sable Island in 54 fathoms (100 m) by a Nova Scotia trawler, February 19, 1937.

The present note records wolffish eggs in abundance at a depth of 70 fath (130 m) over a fairly large area south of LaHave Bank (near lat 40°51′ N, long 64°00′ W). These were taken from March 7 to 11, 1966, in the trawl of the otter trawler *Green Waters*. Approximately 25 tows were made, and Captain Stanley Savage recounted that quantities of 1–4 quarts (1.5–5 liter) were taken on almost every tow. He placed the cluster shown in Fig. 1 in the ship's freezer. This cluster was subsequently sent to the Biological Station at St. Andrews, N.B., for identification.

The eggs shown in Fig. 1 measured 5.8–6.5 mm in diameter. There is no doubt that these eggs are those of *Anarhichas*. There is very little doubt that they could be any other than those of *Anarhichas lupus* L. The embryos measured 16–17 mm in length, and must have been close to hatching. All embryos had large yolk sacs, each with an oil globule. Measurements of egg diameters and embryo lengths corresponded almost exactly to those described by McKenzie and Homans (1937) for *A. lupus* L. (egg diameters, 5.5–6.0 mm; embryos, 17–18 mm). Furthermore, a cruise by the research trawler *A. T. Cameron* in April 1965, close to the area in which the eggs were taken, yielded only *A. lupus* L., 7–91 cm in length (A. V. Tyler, personal communication).

Fishermen occasionally report incidental occurrences of wolffish eggs in their nets. However, the repeated occurrence of eggs in the net of *Green Waters* strongly suggests the region south of LaHave Bank supports a spawning aggregation. To my knowledge, no other such spawning area has been located for this species in Canadian waters.

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(FIG. 1 *opposite*)

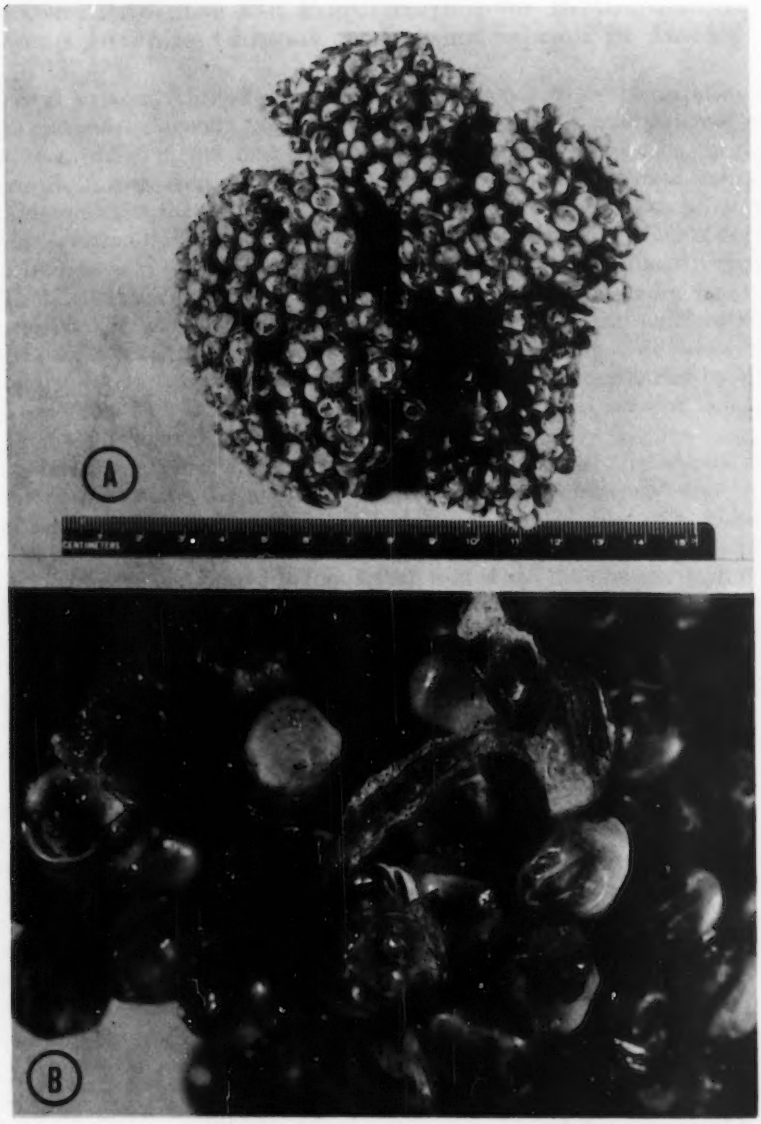

FIG. 1. A, Atlantic wolffish (*Anarhichas lupus* L.) egg cluster about two-thirds of a quart in volume ($\frac{2}{3}$ liter); B, close-up of eggs showing two empty shells and a partially hatched larva.

Powles — J. Fish. Res. Bd. Canada

The Use of Adipose Fin Pigmentation for Distinguishing Between Juvenile Chinook and Coho Salmon in Alaska[1]

Several external characteristics have been proposed for distinguishing between juvenile chinook, *Oncorhynchus tshawytscha*, and coho salmon, *O. kisutch*, (e.g., shape of the anal fin, spacing and shape of parr marks, fin-ray counts, scale counts, etc.). For readily separating coho and chinook salmon in ecological studies at the Chignik lakes, Alaska, these have not proven suitable, as the observation by Meehan and Vania (1961) that the adipose fins of coho salmon from several Alaskan rivers were completely pigmented, whereas those of chinook salmon showed a clear area, generally near the anterior part of the base. We checked this difference in pigmentation in several hundred fish over the past 3 years and found it nearly without fail. In only a few cases was it necessary to resort to the definitive differentiation — the number of pyloric caeca, coho salmon having less than 83 pyloric caeca, and chinook salmon more than 140 (Clemens and Wilby, 1961).

To determine the effect of preservation in formalin on the adipose fin pigment and estimate the accuracy of this method, we recently examined several samples of coho and chinook salmon from the Chignik lakes, Alaska, that had been preserved variously for 10 months to 3 years. The 195 coho salmon used in the test ranged in fork length from 42 to 158 mm (age 0, I, and II) and the 97 chinook salmon from 58 to 135 mm (age 0 and I). The specimens were randomly mixed in a basin filled with water and then individually identified as coho or chinook salmon solely on the basis of pigmentation of the adipose fin (Fig. 1). A count of the pyloric caeca showed that three coho salmon had been identified incorrectly as chinook salmon, or a 1% error in identification had occurred. Pigmentation of the adipose fin did not seem to vary with length of preservation or size of the fish.

A tendency to reversal of this difference of adipose fin pigmentation found in Alaskan stocks was reported by Gregory et al. (1961) for Columbia River coho and chinook salmon smolts; coho salmon had the clear area and chinook salmon were fully pigmented. However, the difference did not provide a positive means of identification and other means were investigated. Pigmentation of the anal fin, they found, is the best characteristic for distinguishing between the two species among Columbia River specimens; coho salmon have black chromatophores concentrated between the fin-rays, resulting in a banded appearance; chinook salmon lack pigmentation in the anal fin.

We noted the presence or absence of anal fin banding in our experimental fish and found that less than 10% were pigmented, and the chromatophores were spread evenly throughout the fin. Moreover, we found a similar pigmentation of the anal fin on the chinook salmon. The pigmentation of the anal fin varied with general coloration of the body rather than with species.

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No single external characteristic has been found to definitely distinguish between coho and chinook salmon. It appears, however, that the pigmentation of the adipose fin complemented with other external characteristics provides a ready means of separating the two species, especially in Alaskan waters.

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(FIG. 1 *opposite*)

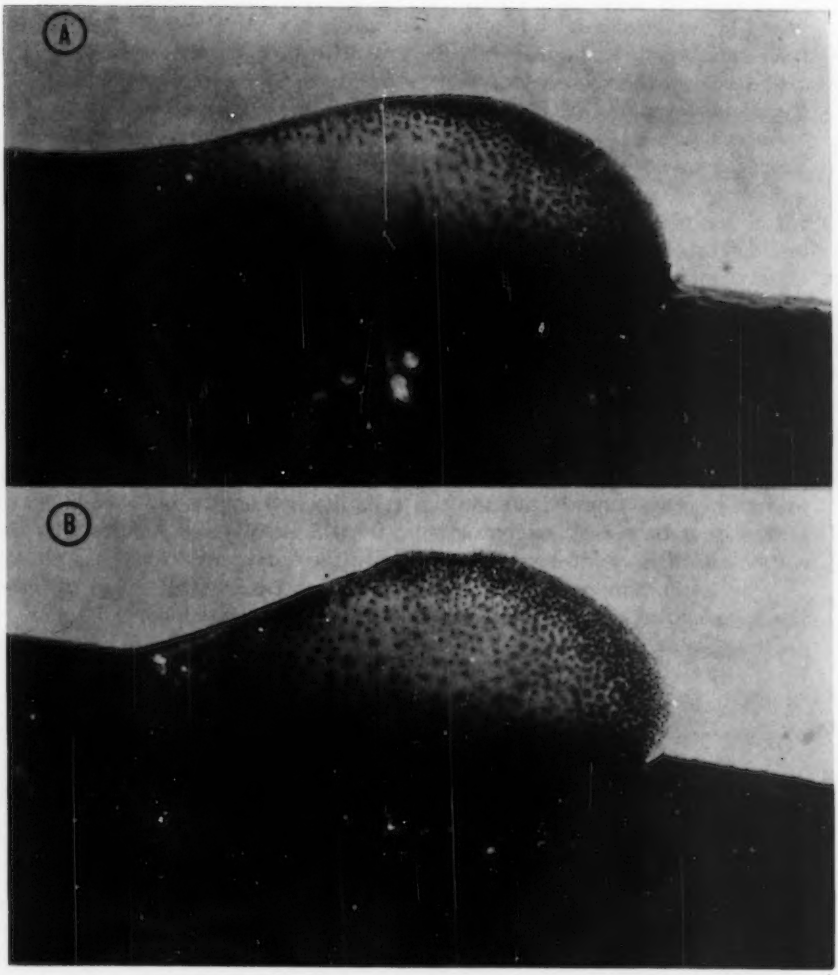

FIG. 1. A, adipose fin of a juvenile chinook salmon (118 mm fork length), showing the clear anterior portion; B, adipose fin of a juvenile coho salmon (115 mm fork length), showing uniform pigmentation.

Dahlberg and Phinney — J. Fish. Res. Bd. Canada

Desiccation of Frozen Fish

In the process of packaging fish products for frozen storage, cellophane inner liners are used by certain fishing companies to minimize desiccation. In an attempt to eliminate the extra time and labour involved in the use of liners, two types of 1-lb cartons, each with and without cellophane liners, were used in a frozen fish storage test to compare their moisture–vapor permeability. The two types of cartons were manufactured from 0.015 calibre solid bleach board with a coating of either polyethylene blend wax (PW) or ethylene vinyl acetate blend wax (EW). Wax overwraps were used on the cartons; MSAT cellophane (0.001 inch) was used for inner liners.

Sole fillets were packaged and frozen under commercial conditions in the respective cartons. The frozen cartons of fillets were stored under adverse conditions at −10 C (14 F) in a laboratory freezer in an attempt to accelerate the development of desiccation; cartons were removed from storage each week to ascertain weight loss. A Mettler 2-kg capacity balance (sensitivity ±0.2 g) was used to determine the weight of each carton of frozen sole fillets. The cartons of frozen fillets were allowed to remain at room temperature for ½ hr during weekly weighings in an attempt to simulate severe conditions of storage such as fluctuating temperatures or improper handling.

Figure 1 presents a representative photograph of 1-lb blocks of frozen sole fillets showing a typical result that was obtained from the use of cartons with and without inner liners after 6 months storage. Desiccation is evident in the frozen block from carton without cellophane inner liner; slight desiccation is evident in the frozen block from carton with cellophane inner liner.

Table I presents results of tests which were made on frozen packaged sole fillets to ascertain the amount of weight lost during a 3-month storage period.

TABLE. I. Extent of desiccation in 1-lb cartons of frozen sole fillets during storage at −10 C (14 F).

Type of carton[a]	Percentage weight loss Months of storage		
	1	2	3
PW	2.1	5.4	7.8
PWC	0.2	0.6	0.7
EW	1.4	4.9	7.7
EWC	0.1	0.4	1.1

[a] PW, polyethylene blend wax; PWC, same as PW with cellophane inner liner; EW, ethylene vinyl acetate blend wax; EWC, same as EW with cellophane inner liner.

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Throughout the storage test it was observed that the loss in weight from frozen fillets packaged with cellophane liners was approximately $\frac{1}{10}$ the amount of weight lost from frozen fillets packaged without cellophane liners. However, it was observed that slight desiccation did develop in a few frozen fillets packaged with cellophane in areas where cellophane did not adequately cover the frozen fillet. The extent of desiccation was similar in the frozen fillets packaged in the two types of cartons without the use of cellophane liners.

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(Fig. 1 *opposite*)

FIG. 1. Photograph showing the extent of desiccation of frozen sole fillets after 6 months storage at −10 C (14 F). Upper block, cellophane inner liner was used in carton; lower block, cellophane inner liner was not used in carton.

Fawn Cusk-eel, *Lepophidium cervinum*, in the Northwest Atlantic

The fawn cusk-eel, *Lepophidium cervinum* (Goode and Bean) 1885, is found along the outer part of the continental shelf from Florida to eastward of Nantucket in depths of 38 to 102 fath (Bigelow and Schroeder, 1953). These authors recorded two specimens, $7\frac{7}{8}$ and $8\frac{1}{2}$ inches long, found in the stomach of a white hake, *Urophycis tenuis*, trawled on Georges Bank (40°31′N lat, 68°55′W long) on June 27, 1951. Goode and Bean (1896) record one specimen taken as far north as off Nantucket Shoals in 76 fath.

Templeman (personal communication) indicates that there are "no records of the (fawn) cusk-eel (*Lepophidium cervinum*) from the Newfoundland area."

During July 17 to August 27, 1965, exploratory fishing was carried on with a 41 Yankee trawl by the stern trawler *Louise P.* along the general 100-fath area from Lydonia Canyon, Georges Bank, northeastward to Sable Island. On four occasions fawn cusk-eels were taken during the four cruises and a total of 192 tows.

Data pertaining to the four specimens are given in Table I. The specimens are in the collections of the Royal Ontario Museum, University of Toronto, Toronto, Ontario — catalogue number 24,064. A fifth specimen was taken on August 14, 1965 at 41°59′N lat, 66°01′W long in 50 fath, bottom temperature 5.2 C, but it was not measured or retained.

These captures extend the range of this species almost 200 miles northward.

TABLE I. Data pertaining to four specimens of fawn cusk-eel.

Specimen No.	Length (*mm*)		Sex	Vertebrae	Date of capture	Depth of capture (*fath*)	Bottom emp+ (*C*)	Position
	Total	Standard						
1	245	233	♀	73	July 19, 1965	100	7.8	41°03′N, 66°28′W
2	227	217	♂	74	July 19, 1965	65	9.1	40°45′N, 66°55′W
3	251	239	♂	73	July 20, 1965	100	9.0	40°41′N, 66°55′W
4	231	220	♀	74	July 20, 1965	100	9.0	40°41′N, 66°55′W

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The four specimens were examined by Dr W. B. Scott, Curator, Department of Ichthyology and Herpetology, Royal Ontario Museum, who kindly provided the data on length, sex, and vertebral number.

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Predation on Living Fishes on Longline in Baffin Bay by the Amphipod *Eurythenes gryllus* (Lichtenstein), and a New Distribution Record

In a bottom longline set by the *A. T. Cameron*, August 4, 1965 in the deep channel of Baffin Bay, several nautical miles from the "West Ice," with the author as scientist-in-charge, a large female *Raja hyperborea*, 76 cm in length, was taken which had almost all the pelvic fins eaten away ventrally. Four large red amphipods (Fig. 1) were attached to this partly eaten pelvic area and at least three additional large red amphipods of this type dropped off and were lost in the sea when this skate was being pulled over the rail. Two eelpouts, estimated to be about 30 cm long, were eaten except for the bony jaws, completely devoid of flesh, which remained on the hooks. All baits (squid) except two were eaten from about 480 hooks attached 3.7 m apart.

The amphipods (Fig. 1) were *Eurythenes gryllus* (Lichtenstein) 1822 and were 46, 43, 43, and 32 mm in length, head to the most posterior point, whether uropods or telson, measured at natural preserved flexion, and 53, 52, 46, and 36 mm in maximum extended length, between the same points. These amphipods may reach a length of 90 mm (Stephensen, 1933) and a specimen 4½ inches (ca. 114 mm) in length has been reported by Smith (1884). Shoemaker (1956) reports a 95-mm *E. gryllus* taken by the *Albatross* off Chesapeake Bay at 3500 m. The general position "off Chesapeake Bay" agrees with the position given by Smith (1884) for his 4½ inch (114 mm) specimen of *E. gryllus* and the year of capture (1883) and the depth are the same. Presumably this was the specimen of 4½ inches reported by Smith (1884). Shoemaker also reports *E. gryllus* as reaching 100 mm so that although he does not mention Smith (1884) he evidently disregards Smith's measurement of 114 mm.

Dr Thomas E. Bowman of the Smithsonian Institution, United States National Museum, has written me (August 8, 1966) that there can be no doubt that Smith's and Shoemaker's specimens are the same, and that this specimen from *Albatross* station 2097, USNM Cat. No. 5480 measures 96 mm when fully extended but not distorted. This measurement is from the anterior margin of the head to the end of the uropods. The antennae are about 12 mm long so that if they are included in the total length it comes close to Smith's 4½ inches. Smith must have measured the animal before preservation or including the antennae, or both.

The line was down for 6 hr and considering the depth and the weights used the baits were probably not on bottom for more than half of this time. The hooks were small. As a rule, large demersal fish do not die naturally in this short period attached to a longline and judging from the rapidity of destruction the fish must have been attacked by swarms of the amphipods shortly after becoming attached to the hook and while alive.

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It is most likely that this is another example of amphipods attacking and eating living marine animals as in Hart (1942) for *Anonyx nugax* eating herring and cod in live boxes, Templeman (1954, 1958) for *Orchomenella pinguis* preying on live lobsters, and Scarratt (1965) for *Anonyx* sp. attacking live lobsters. Presumably if the fish had not been attached to the hooks and had been free to move normally they would not have been attacked successfully. Probably also, the odour of the blood from the hook wounds attracted the amphipods.

These amphipods agreed generally with the description of *Eurythenes gryllus* (Sars, 1895) and with the additional details described by Stephensen (1933) and Barnard (1961). There are, however, some points of distinction with previous descriptions, especially that of Sars.

The upper hind corner of the most posteriorly projecting part of the coxal plate of peraeopod 4 (7 peraeopods in our description of which No. 1 and 2 are modified as gnathopods 1 and 2) is rounded in our specimens (Fig. 1) and not incipiently pointed as in Sars' plate 30. This rounding is less evident in the smallest specimen. The rounding of the posterior corner of this plate is also shown in Barnard's (1961) drawings of *E. gryllus*.

In our specimens, as in Lilljeborg (1865) and in Stephensen's (1933) addition to Sars' (1895) description, the lower hind corner of the epimeral plate of pleon segment No. 2 is mucronate at the postero-ventral angle, with an oblique ridge across the plate. Also, on pleon segment No. 1 there is usually a slight projection of a similar nature, and a similar ridge across the plate (Fig. 2). This ridge is figured but not mentioned by Stephensen and is shown in Barnard (1961).

Our four specimens agree in the length of the dactyls of peraeopods 5–7 and in other characteristics (Figs. 1, 3) with the female of *E. gryllus* illustrated in Sars (1895) and not with *Eurythenes obesus* (Chevreux). Also, the dactyls of peraeopods 5–7 are short. In one of the larger female specimens or which these proportions were measured, the dactyls of peraeopod 5 are only 40% as long as article 6 (propodite) and the combined length of articles 3–7 on the fifth peraeopod is three times as long as article 2. These proportions agree with *E. gryllus* and not with *E. obesus* in Barnard (1961).

The three larger specimens were females. The smallest specimen was a male with genital papillae on the sternite of the most posterior thoracic segment.

The appendages (Fig. 3) agree with the descriptions for *E. gryllus* in Sars (1895), Stephensen (1933), and Barnard (1961).

Our specimens also add to the knowledge of the distribution of this species. In the Northwest Atlantic it is recorded from off the east coast of North America, 37°56′20″N and 70°57′30″W at about 3500 m (Smith, 1884); from Umanak Fjord in West Greenland at about 70°30′ N; off the west coast of Greenland between 60 and 64°N pelagically over depths of 839–1600 m; and in the Labrador Sea, 62°19′N, 56°00′W pelagically over a depth of 2550 m and at 56°56′N, 51°17′W pelagically over a depth of 3500 m (Stephensen, 1933).

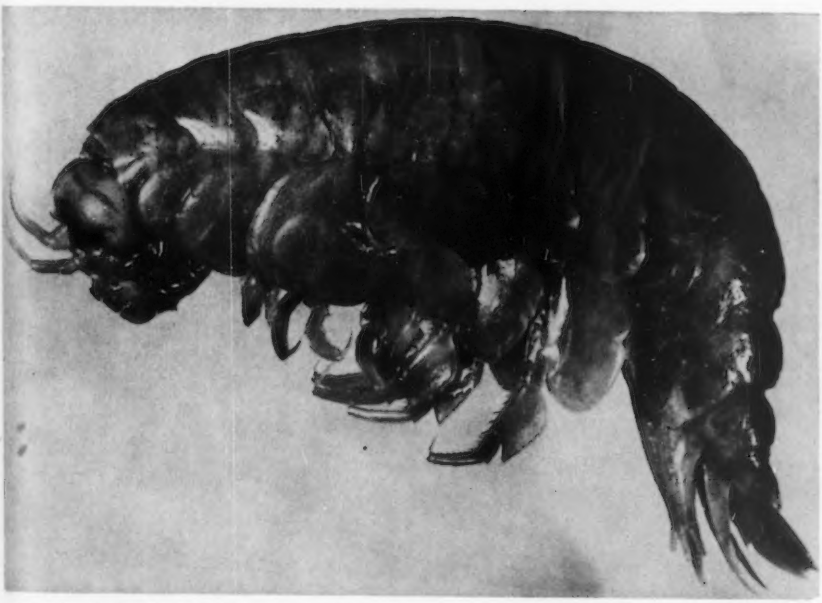

FIG. 1. Lateral view of female *Eurythenes gryllus* × 3 from Baffin Bay, August 4, 1965.

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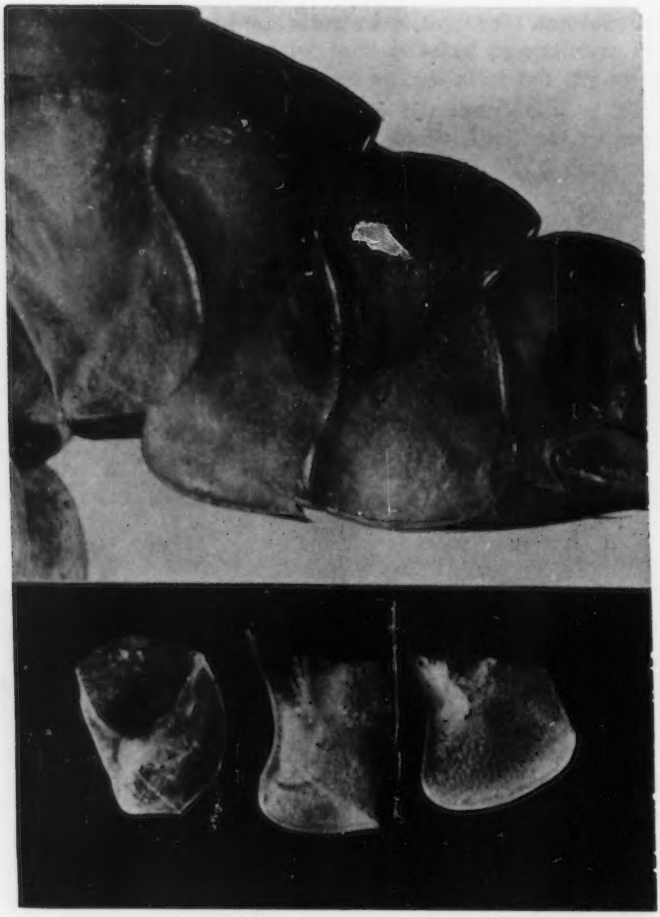

FIG. 2. Lateral views of *Eurythenes gryllus* from Baffin Bay, August 4, 1965: above, pleon segments 1–4 × 7.6; below, epimeral plates of pleon segments 1–3 × 5.7.

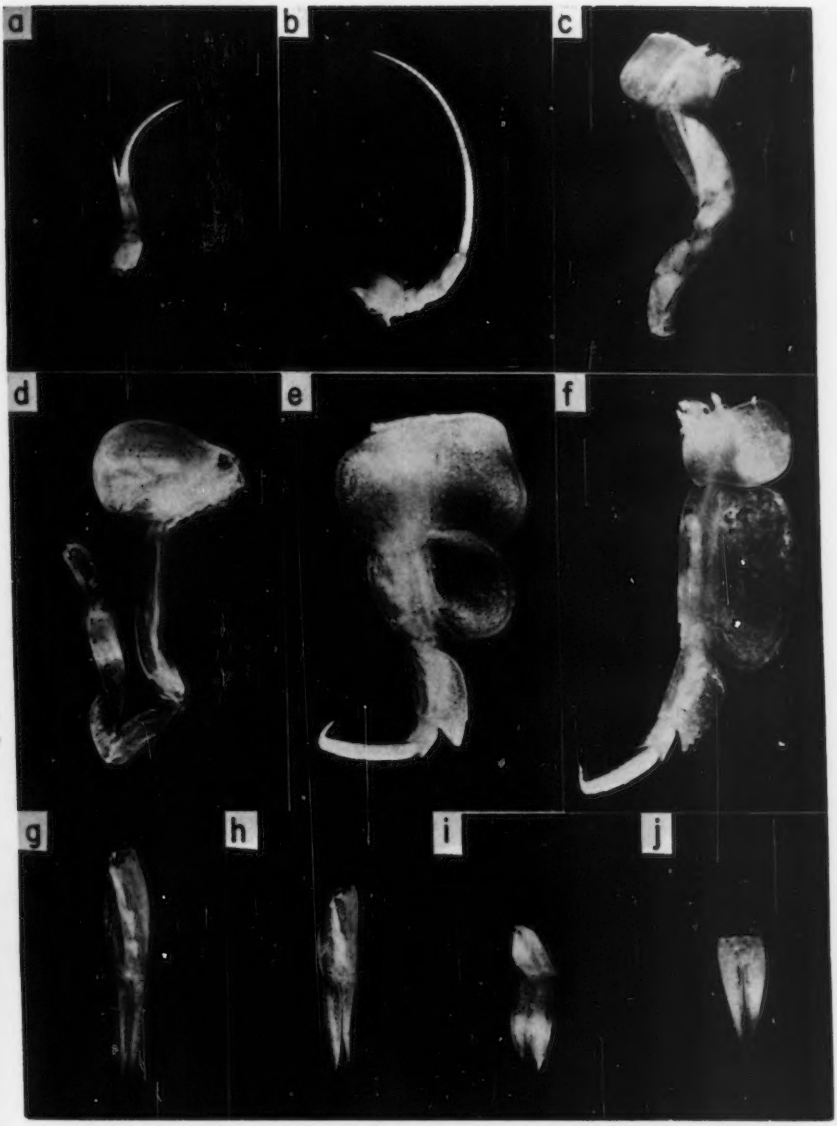

FIG. 3. Appendages of female *Eurythenes gryllus* (52 mm in maximum extended length) × 4 from Baffin Bay, August 4, 1965: *a*, antenna 1, left; *b*, antenna 2, left; *c*, gnathopod 1, left, lateral view; *d*, gnathopod 2, left, lateral view; *e*, peraeopod 5, left, lateral view; *f*, peraeopod 7, left, lateral view; *g*, uropod 1, right, posterior view; *h*, uropod 2, right, posterior view; *i*, uropod 3, right, posterior view; *j*, telson, dorsal view.

Our records from Baffin Bay, at 68°07′30″N, 60°49′W from the bottom at 1650 m, −0.26 C, are more westerly in Baffin Bay than the previous records which we have noted in the literature. The new records are from the middle of the deep channel in Baffin Bay but much closer to the Canadian than to the West Greenland coast.

I am grateful to Dr H. J. Squires of the St. John's Station, Dr Thomas E. Bowman of the United States National Museum, Washington, D.C., and to Dr M. J. Dunbar, Marine Sciences Centre, McGill University, Montreal for information and advice in relation to details of this paper.

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Copies of individual reprints, if available, may be obtained from the authors or Board establishments through which the investigations were conducted.

Reprints of these articles are included in an annual volume of "Studies," composed of two parts. These are distributed to a selected mailing list. (Articles numbered 1020 to 1109 appeared in the Studies for 1966, Part 2.)

Guide to Contributors

Journal of the Fisheries Research Board of Canada

The *Style Manual for Biological Journals*, 2nd edition, published by the American Institute of Biological Sciences, 2000 P Street NW, Washington, D.C., has been adopted as the guide to authors. *Webster's Third New International Dictionary* is the standard for spelling and division of words in English; *le Grand Larousse Encyclopédique*, for those in French. Exceptions are made for papers that follow the *Oxford English Dictionary* entirely. For readability and appeal, writing must be clear, logical, and precise.

STYLE AND ORGANIZATION

Original research papers should conform as far as possible to the following pattern, although unnecessary standardization is not desired:

Title must be kept short, specific, and informative for retrieval systems. Subtitles and series papers should be avoided.

Abstract must be complete in itself. It should be informative in scope, methods, and results; briefly indicate significance of the findings; be free of unnecessary description; and not exceed 200 words. Authors are encouraged to provide an abstract in both languages; one must be provided in the same language as the text.

Introduction should outline the problem, referring only to pertinent investigations, and define the objectives or reasons for the study.

Materials and methods or *Experimental procedures* should include a description of design and organization of the investigation. Procedures, including those for statistical analyses of data, must be either referenced or described in enough detail to permit the work to be repeated.

Results are preferably separated from discussion. The text must be meaningful without reading of tables, illustrations, or other research; these should be referred to in parentheses. Only data necessary to support the text should be given. Data must not be duplicated in tables and in illustrations, and should be summarized so that they can be easily understood. Statistical analyses should be used when appropriate to aid in interpreting the data, but should not mask the comparisons of interest. Inclusion of preliminary or raw data, even in an appendix, is discouraged. Measurements should be reported in metric units.

Discussion should give the significance of the findings, and their relation to published research. Importance of this section cannot be overemphasized.

Conclusions as a separate section are optional.

Acknowledgments, if included, are placed at end of text.

References should be listed alphabetically by author, without numbers, in the form described by the *Style Manual for Biological Journals*. Citations in the text are made by the *name-and-year* system. Manuscript reports may be listed in the References, but should be cited in the text with the letters "MS" preceding the year.

Notes are for publishing research with narrow boundaries that may result as a by-product of investigations, for describing research techniques and fishing methods, for establishing publication priority, and for reporting useful information from projects that were terminated before completion. This section is not a repository for inferior research. If the scope of the Note permits,

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Review articles should include an abstract, assess the state of research and knowledge on the subject, and be organized under a logical sequence of topics.

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Authors, typists, and draftsmen are urged to follow the more detailed instructions for preparing copy in the *Style Manual for Biological Journals*.

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Line drawings should be made with black india ink or printed transparent overlays on white drawing or tracing paper. Coordinate paper with orange, yellow, green, or red grids **must not** be used. All lines, symbols, letters, and numerals must be neat, and of the appropriate size for the desired reduction. Do not use typewriting. Two or more drawings should be grouped wherever possible, making full use of space available. In full-page illustrations, the ratio of width to height should conform to that of the Journal page (5 by 7.5 inches) with allowance for captions. Captions for illustrations should be typed on a separate sheet (or sheets) at the end of the manuscript, and each illustration must be identified. Size of illustrations ordinarily should be 8.5 by 11 inches or less.

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